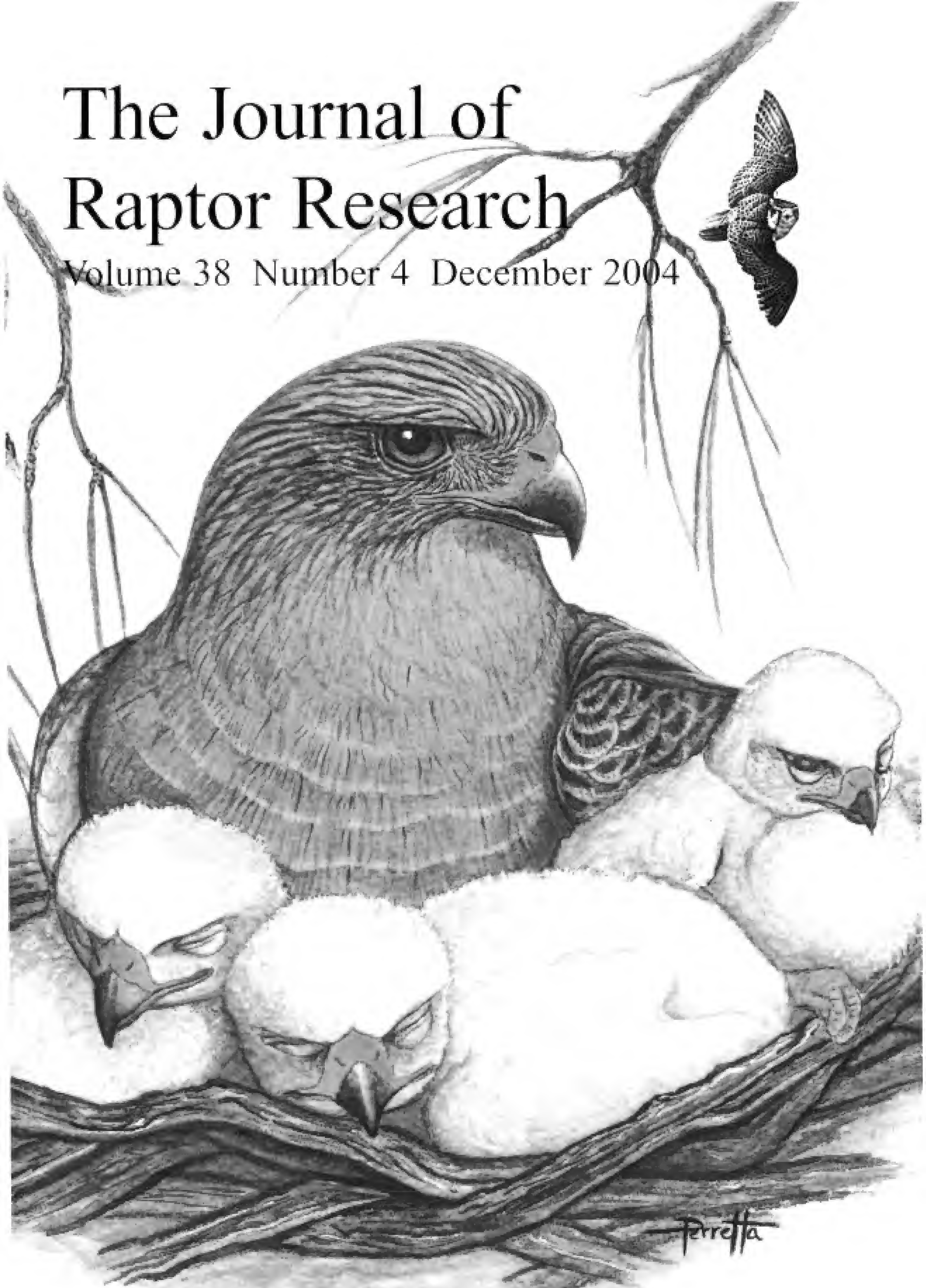


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COVER: Nesting Red-shouldered Hawk (*Buteo lineatus*). Painting by Nicole Perretta; for more information and images, visit www.hawkandjaguar.com

CONTENTS

RESPONSES OF NESTING BALD EAGLES TO EXPERIMENTAL PEDESTRIAN ACTIVITY. James W. Watson	295
DISPERSAL AND MORTALITY OF RED-SHOULDERED HAWKS BANDED IN OHIO. Cheryl R. Dykstra, Jeffrey L. Hays, Melinda M. Simon, John B. Holt, Jr., G. Ronald Austing, and F. Bernard Daniel	304
DECREASES IN A POPULATION OF RED-SHOULDERED HAWKS NESTING IN CENTRAL MARYLAND. Elwood M. (Woody) Martin	312
SEASONAL VARIATION IN SEX RATIO OF NESTLING ELEONORA'S FALCONS. Dietrich Ristow and Michael Wink.....	320
TAWNY FISH-OWL PREDATION AT FISH FARMS IN TAIWAN. Yuan-Hsun Sun, Hsin-Ju Wu, and Ying Wang.....	326
GEOGRAPHIC VARIATION IN MORPHOLOGY OF FOUR SPECIES OF MIGRATORY RAPTORS. Elise Vernon Pearlstine and Daniel B. Thompson	334
HOME-RANGE SIZE OF THE JAVAN HAWK-EAGLE (<i>SPIZAETUS BARTELSI</i>) ESTIMATED FROM DIRECT OBSERVATIONS AND RADIOTELEMETRY. Jan Ove Gjershaug, Nils Røv, Torgeir Nygård, Dewi M. Prawiradilaga, M. Yayat Afianto, Hapsoro, and Adam Supriatna	343
POPULATION STATUS AND REPRODUCTIVE PERFORMANCE OF EURASIAN GRIFFONS (<i>GYPES FULVUS</i>) IN EASTERN SPAIN. Pascual López-López, Clara García-Ripollés, and José Verdejo	350
SHORT COMMUNICATIONS	
GENDER DETERMINATION IN THE SWAINSON'S HAWK (<i>BUTEO SWAINSONI</i>) USING MOLECULAR PROCEDURES AND DISCRIMINANT FUNCTION ANALYSIS. José Hernán Sarasola and Juan José Negro	357
PRODUCTIVITY AND FLEDGLING SEX RATIO IN A CINEREOUS VULTURE (<i>AEGYPIUS MONACHUS</i>) POPULATION IN SPAIN. Auxiliadora Villegas, Juan Manuel Sánchez-Guzmán, Emilio Costillo, Casimiro Corbacho, and Ricardo Morán	361
NEST PROVISIONING OF THE ORIENTAL HONEY-BUZZARD (<i>PERNIS PTILORHYNCHUS</i>) IN NORTHERN TAIWAN. Kuang-Ying Huang, Yao-Sung Lin, and Lucia Liu Severinghaus.....	367
WINTER DIET OF THE GREATER SPOTTED EAGLE (<i>AQUILA CLANGA</i>) IN THE AMVRAKIKOS WETLANDS, GREECE. Haralambos Alivizatos, Dimitris Papandropoulos, and Stamatis Zogaris	371
GENDER DETERMINATION OF EURASIAN EAGLE-OWLS (<i>BUBO BUBO</i>) BY MORPHOLOGY. Maria del mar Delgado and Vincenzo Penteriani	375
LETTERS	
A POSSIBLE CASE OF DOUBLE BROODING OF EAGLE-OWLS (<i>BUBO BUBO</i>) IN SPAIN. Joaquín Ortego	378
INSECT HAWKING OBSERVED IN THE LONG-EARED OWL (<i>ASIO OTUS</i>). Darren J.H. Sleep and Rowan D.H. Barrett	379
OSPREY SCAVENGES COMMON MURRE CARCASS IN COASTAL WASHINGTON. Joseph B. Buchanan	380
HOW LONG IS TOO LONG? A CASE OF FOSTERING NESTLING BONELLI'S EAGLES (<i>HIERAAETUS FASCIATUS</i>). Satish A. Pande, Amit P. Pawashe, Banda Pednekar, Anil Mahabal, and Reuven Yosef	381
INFORMATION FOR CONTRIBUTORS	383
INDEX TO VOLUME 38.....	387

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RESPONSES OF NESTING BALD EAGLES TO EXPERIMENTAL PEDESTRIAN ACTIVITY

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ABSTRACT.—In 1993 and 1994, I tested effects of pedestrian activity on Bald Eagles (*Haliaeetus leucocephalus*) at nests on 21 territories in western Washington. A pedestrian walked around each nest 10 min/hr for 6 hr during 65 trials. Eagles averaged 8.0 ± 1.8 (SE) responses/trial (i.e., per hr of pedestrian activity, $N = 524$ combined responses), and 10.7 ± 2.0 min of response time/trial ($N = 681$ min combined response time). Responses accounted for $23 \pm 3\%$ by frequency, and $3 \pm 0.3\%$ by time, of all perch behaviors on treatment days. I observed no damage or injury to eggs or young from the encounters, although nest flushes had a mean of 3.1 ± 0.9 responses/trial. Treatments resulted in a two-fold increase in mean egg exposure time/trial ($\bar{x} = 7.8 \pm 1.6$ min/exposure) compared to controls ($\bar{x} = 3.3 \pm 0.8$ min/exposure). Precipitation reduced the time adults left eggs and young exposed from a mean of 7.9 ± 0.9 min/hr to 5.1 ± 1.0 min/hr on control days. Nest height, nest screening, pedestrian distance, and phenology affected eagle responses; responses were substantially reduced at nests that were >40 m high and highly-screened, when pedestrian distance to nests increased from 60–120 m, and during incubation compared to the brood period. To reduce risks from increased exposure of eggs and young, I recommend that pedestrian activities be restricted near Bald Eagle nests during incubation and the first 3 wk of brooding. For Bald Eagle nests in forested, non-pristine areas of residential development, pedestrian activity less than 120 m from nests can be restricted as a function of nest height and screening to minimize disturbance.

KEY WORDS: *Bald Eagle; Haliaeetus leucocephalus; behavior; disturbance response; human activity; Washington.*

RESPUESTA DE *HALIAEETUS LEUCOCEPHALUS* NIDIFICANTES ANTE ACTIVIDAD PEATONAL EXPERIMENTAL

RESUMEN.—En 1993 y 1994, evalué los efectos de la actividad de peatones sobre águilas *Haliaeetus leucocephalus* en nidos ubicados en 21 territorios en el oeste de Washington. Un peatón caminó alrededor de cada nido 10 min/hr por 6 hr durante 65 ensayos. Las águilas presentaron en promedio (\pm SE) 8.0 ± 1.8 respuestas por ensayo (i.e., por hora de actividad peatonal, $N = 524$ respuestas combinadas), y 10.7 ± 2.0 min como tiempo de respuesta/ensayo ($N = 681$ min combinando el tiempo de respuesta). Del total de comportamientos de percha en los días de estudio, las respuestas correspondieron al $23 \pm 3\%$ en términos de frecuencia y al $3 \pm 0.3\%$ en términos de tiempo. No observé daños o lesiones en los pichones o huevos como consecuencia de los encuentros, aunque en promedio las aves fueron espantadas del nido en 3.1 ± 0.9 ocasiones por ensayo. Los tratamientos condujeron a un incremento del doble en el tiempo promedio de exposición de los huevos ($\bar{x} = 7.8 \pm 1.6$ min/exposición) en comparación con controles ($\bar{x} = 3.3 \pm 0.8$ min/exposición). La precipitación redujo el tiempo por el cual los adultos dejaron expuestos los huevos y pichones de un promedio de 7.9 ± 0.9 min/hr a 5.1 ± 1.0 min/hr en días de control. La altura del nido, su nivel de protección, la distancia al peatón y la fenología afectaron la respuesta de las águilas; las respuestas fueron sustancialmente reducidas en nidos que estaban ubicados a más de 40 m de altura y altamente protegidos, cuando la distancia al peatón se

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incrementó de 60–120 m, y durante la incubación, en comparación con el período de empollamiento. Para reducir los riesgos del incremento en la exposición de los huevos y pichones, recomiendo que las actividades peatonales sean restringidas cerca de los nidos de *H. leucocephalus* durante la incubación y las tres primeras semanas de cría de los pichones. Para áreas forestales no prístinas con desarrollo residencial, la actividad de los peatones a menos de 120 m de los nidos puede restringirse en función de la altura y protección de los nidos para minimizar el disturbio.

[Traducción del equipo editorial]

As Bald Eagle (*Haliaeetus leucocephalus*) populations recover, increasing numbers of eagles are nesting in landscapes subject to human activities and habitat alteration. Post-recovery persistence of some populations, such as in Florida and the Chesapeake Bay region, may be directly tied to the ability of eagles to reproduce successfully in urban and residential environments (Buehler et al. 1991). Human impacts are common in Washington, where in the past 25 yr increasing eagle populations and residential development in Puget Sound led to the development of >1150 eagle management plans with private landowners (Stinson et al. 2001). Management plans attempt to minimize effects of human activities primarily by imposing restrictions near nests during the nesting period, maintaining nest screening, and maximizing distances between human activities and nesting eagles. The effectiveness of management planning depends on our ability to understand how Bald Eagles respond to human activities near residential developments.

Behavioral changes of Bald Eagles that might precede nest failure often are not studied because they are difficult and time-consuming to assess (Anthony and Isaacs 1989). Human activities can change behavior of nesting eagles through auditory and visual disturbance (Grier 1969, Fraser et al. 1985, Grubb and King 1991, Steidl and Anthony 1996). Such activities may cause reductions in incubation time, brooding time, feeding time, and other adult behaviors that affect attendance of eggs or young, and potentially survival of young. These changes in adult behavior may be possible indicators of impending nest failure of raptors (Holthuijzen et al. 1989).

Experimental studies of human activities on Bald Eagles provide an opportunity to understand how eagles respond to different types of disturbance and variable disturbance parameters (e.g., distance) in controlled situations. Fraser et al. (1985) were first to evaluate experimentally flush distances of nesting Bald Eagles in response to a pedestrian approaching the nest directly, and made recommendations for buffer zones based on those

distances. McGarigal et al. (1991) experimentally tested responses of foraging eagles to stationary boating activity and demonstrated that Bald Eagles were affected by passive human activities. More recently, in interior Alaska, Steidl and Anthony (2000) found experimental recreational activity resulted in significant behavioral changes to Bald Eagles nesting, potentially leading to reduced nestling survival.

To better understand the impact of human activities on behavior and reproduction of Bald Eagles in rural areas undergoing residential development, I conducted an experiment in western Washington in 1993–94. I used a walking pedestrian to simulate the most common human activity in the rural environment, and recorded the frequency and duration of Bald Eagle responses to the pedestrian during different nest stages, at different nest heights, with different degrees of screening cover, and at varying distances from nests. Analysis of these factors provided guidelines for reducing the effects of human activity in areas of residential development.

STUDY AREA

The Puget Sound region in northwest Washington is characterized by diverse saltwater, brackish, and freshwater ecosystems. Bald Eagles nest in coniferous stands dominated by Douglas-fir (*Pseudotsuga menziesii*) along marine shorelines, and in riparian stands dominated by black cottonwood (*Populus trichocarpa*) along lakes and rivers. Nests are typically placed in dominant or codominant trees in forest stands. High annual precipitation (e.g., 100–150 cm) results in closed forest canopies and dense understories, except where stands have been recently logged, or trees have been limbed. Thus, visibility of human activities from eagle nests varies. Land development in recent years has resulted in increased residential activities near nesting eagles (D. Stinson, J. Watson, and K. McAllister unpubl. data). The statewide Bald Eagle population has increased exponentially in the past 25 yr and growing numbers of eagles are nesting along Puget Sound (Watson et al. 2002), where humans commonly approach within 400 m of Bald Eagle nests (unpubl. data).

METHODS

Eagle responses to human activity were assessed by comparing eagle behaviors when a pedestrian was pres-

ent (treatments) and absent (controls). Six-hour treatments and controls were applied to each eagle nest on consecutive days beginning at dawn. The order of each trial was randomized (treatment-control vs. control-treatment). During each treatment, a person walked a circular path around the nest tree once/hr (i.e., six times/treatment) to simulate naturally occurring pedestrian activity near the eagle nest, as opposed to direct nest approaches which are atypical (pers. obs.). An observer recorded the following information: duration (sec) of the pedestrian activity; frequency, duration, and type of eagle disturbance responses (i.e., none, flush and perch, perch, vocalize, return flight to nest, fly in and respond, surveillance flight, flush and soar, flush and respond, redirected aggression toward conspecific); and perch locations and flight paths of eagles on 1:12000 aerial photos. Photos were used for measuring the distance of the eagle to the pedestrian at the point of response. On both control and treatment days the observer recorded time and duration (sec) of all behaviors for both adult eagles <200 m from the nest tree (i.e., nest building, incubating, brooding, feeding young, resting), and at distances >200 m where visibility allowed. Behavior frequencies and duration were summed for both adults on each territory because response was sometimes cued by the behavior of the other adult. Wind speed (low = calm or slight breeze; high = brisk or gusty winds), cloud cover ($\leq 50\%$ vs. $> 50\%$), and precipitation (yes/no) were recorded.

I conducted trials (i.e., one control-treatment on consecutive days) at a 60-m radius from each nest once during incubation and once during the first 3 wk of brooding (i.e., 42 trials). Trials conducted at the same nest were separated by >5 wk to minimize possible effects of repeated treatments (e.g., habituation) on responses. To assess the effect of pedestrian distance, I repeated the experiment at the seven nests with partial screening during incubation and brooding at 30 and 120 m (i.e., 28 trials). This resulted in a total of two trials/nest at each of the three distances. I standardized the total time and distance traversed by pedestrians among treatments by walking the circumference of the 120-m distance once, the circumference of the 60-m distance twice, and circumference of the 30-m distance four times. Duration of pedestrian activity was ca. 10 min long (\bar{x} duration = 9.0 ± 2.5 min [SD]) for a total of 60 min of activity/6-hr treatment, with variability due to differences in ground cover and topography.

I described screening cover at nests by scoring nest visibility as high (0), partial (50), and low (100) at 30 m, 60 m, 120 m, and 200 m along four transects at each cardinal direction from the nest. Screening was assessed prior to leafout in January and after leafout in May, and categorized by the mean score as: ≤ 33 = little or no screening; 34–66 = partial screening; or ≥ 67 = high screening. Seven nests were identified for each screening category. Height of each nest was measured with a clinometer and categorized (20–29 m, 30–39 m, 40–49 m, >49 m) for analysis.

Nests on 21 Bald Eagle territories were studied; 12 adjacent to Puget Sound, six along rivers, and three at lakes. These were randomly selected from 323 nests with one to five homes <400 m away, which was typical of human

activity levels near eagle nests in Puget Sound. I did not select nests that were at remote locations isolated from human activities because my intent was to provide recommendations for Bald Eagles with moderate prior exposure to human activity. Nests were chosen in settings with varied vegetative screening that still afforded an observer, stationed >400 m away, good visibility of the area <200 m from the nest tree.

Data Analysis. I summarized the frequency and duration of eagle disturbance responses and perch behaviors during controls and treatments by computing the grand mean and standard error from means computed at each nest. Paired *t*-tests were used to evaluate the significance of changes in responses and behaviors between controls and treatments.

I used multivariate analysis of variance to test effects of nest height, nest screening, distance to pedestrian, and nest phenology on standardized frequencies and durations of three eagle disturbance responses (total responses, nest flushes only, and combined nest responses including flushes, perch alert, and vocalization) and six eagle behaviors (perching <200 m from nest, nest building, incubation, brooding, feeding young, resting). Effects of treatments on eagle responses and behaviors were computed as the arithmetic difference between controls and treatments. I tested full models that included interactive effects. If no interactions were identified ($P \geq 0.10$), effects found to be significant were tested in reduced models, and factor level effects were identified with the Bonferroni's method (Miller 1981).

I used *t*-tests to compare mean exposure time (sec) for eggs and young on control days, on treatment days while the pedestrian was present, and on treatment days after the pedestrian activity. Also, *t*-tests were used to compare exposure times (sec) for eggs and young on control days among categories of precipitation, wind, and cloud cover. I did not assess the effects of weather on egg and young exposure during pedestrian activity because I intentionally avoided conducting trials on days with inclement weather. Repeated measures analysis of variance was used to assess if eagles habituated to treatments among the six exposures to the pedestrian on treatment days.

Where appropriate, variables were tested to verify the assumption of normality. No transformations were necessary for variables deemed significant in final models. Significance level for all tests was $\alpha = 0.05$.

RESULTS

Behavioral Responses. I conducted 65 of 70 scheduled trials during the 2-yr study (nest failures eliminated five brooding trials). Disturbance responses accounted for $23 \pm 3\%$ (SE) by frequency and $3 \pm 0.3\%$ by time, of all behaviors on treatment days. Eagles had a mean of 8.0 ± 1.8 disturbance responses/nest for each trial, or each hr of pedestrian activity ($N = 524$ combined responses). The typical response sequence was a flush from the nest, followed by re-perching on the nest, and eventual resumption of pretreatment perch behavior. Eagles flushed and perched a mean of 3.1 times/

Table 1. Bald Eagle responses to experimental pedestrian activity in northwestern WA, 1993–94. Response rates (number of responses/nest, $N = 21$) are standardized per trial (1 hr of pedestrian activity).

RESPONSE	FREQUENCY/hr		DURATION (sec/hr)	
	MEAN	SE	MEAN	SE
Flush and perch	3.1	0.9	123.2	39.1
Perch or vocalize	2.7	0.9	271.4	67.8
Return flight to nest	1.1	0.3	74.2	29.5
Fly in and respond	0.2	0.1	25.2	12.1
Surveillance flight	0.2	0.1	64.1	56.3
Flush and soar	0.1	0.1	37.4	23.8
Flush and respond	0.2	0.1	8.3	3.8
Redirected aggression	0.2	0.1	33.0	22.8

nest (± 0.9) during each trial (Table 1). Eagles averaged 10.7 (± 2.0) min of response time/nest for each hr of pedestrian activity ($N = 681$ min combined response time), and typically perched or vocalized half of that time (Table 1).

Eagles were initially perched on the nest a mean of $48 \pm 1\%$ of time when pedestrian activity was initiated during trials. For eagles on nests, the mean encounter distance for flush responses was 76 ± 9 m/nest, and 72 ± 9 m/nest for combined responses. For eagles perched anywhere on the territory, the mean encounter distance for flush responses was 72 ± 10 m/nest, and 71 ± 10 m/nest for all responses.

Pedestrian activity caused changes in eagle behavior, manifested as increased frequency of combined perch behaviors < 200 m from nests (Table 2). Accordingly, frequency of pedestrian-induced responses increased, while frequency of nest building decreased. Pedestrian activity had less of an effect on duration of combined behaviors (Table 2). Although incubation time per trial was not reduced by pedestrian activity, duration of individual egg exposures/trial was longer ($t = 3.39$, $P = 0.009$, $N = 21$) during treatments ($\bar{x} = 7.8 \pm 1.6$ min/exposure; range = 0.3–59.0) compared to controls ($\bar{x} = 3.3 \pm 0.8$ min/exposure; range = 0.1–110.2), and was also longer ($t = 9.25$, $P < 0.0001$) than egg exposures immediately after treatments ($\bar{x} = 1.9 \pm 0.5$ min/exposure; range = 0.1–27.1). Mean duration of posttreatment egg exposure was partially dependent on mean duration of treatment exposure; eagles reduced posttreatment egg exposures by 30 sec for every 5 min increase in egg exposure during treatments (linear regression, $r = 0.29$, $P = 0.018$). During incubation, eagles responded a mean of $23 \pm 5\%$ of the

time the pedestrian was present (14 ± 3 sec/min of experimental human activity). Total brood time decreased due to pedestrian activity (Table 2), but time that young were exposed/trial during the brood period was the same ($P = 0.101$) for treatments ($\bar{x} = 33.1 \pm 9.4$ min/exposure; range = 1.3–316.7), controls ($\bar{x} = 35.4 \pm 14.1$ min/exposure; range = 0.1–360.0), and immediately after treatments ($P = 0.432$; $\bar{x} = 29.5 \pm 11.4$ min/exposure; range = 0.1–319.4). For nests with young ($N = 19$), eagles responded a mean of $43 \pm 10\%$ of the time the pedestrian was present (26 ± 6 sec/min).

I did not observe direct effects to eggs due to treatments (e.g., eggs rejected or broken by flushing adults). Hatching success was unaffected at a nest where eggs were exposed for 59 min. Direct effects from weather were mixed; total time eggs and young were exposed was higher ($t = 2.05$, $P = 0.045$) in the absence of precipitation (7.9 ± 0.9 min exposure/hr) than when there was some level of precipitation (5.1 ± 1.0 min exposure/hr). There was no effect of wind ($P = 0.325$) or cloud cover ($P = 0.370$) on exposure time. Nest success averaged 1.14 young/occupied territory during the experiment, and 1.11 young/occupied territory in 1994, the year following the experiment. All nine territories treated in 1993 were reoccupied in 1994.

The presence of other raptors increased eagle responsiveness. Seventy-eight encounters with conspecifics and four encounters with Red-tailed Hawks (*Buteo jamaicensis*) were recorded during trials. Sixty-six encounters (85%) with other eagles involved a non-incubating or non-brooding adult chasing an intruder. Eight encounters (10%) were of an incubating or brooding bird vocalizing or standing above the eggs or young in response to

Table 2. Effects of pedestrian activity on the frequency and duration of Bald Eagle behaviors during 65 experimental trials. Each trial consisted of a 6-hr control and a 6-hr treatment in which pedestrian activity was conducted <200 m away for 10 min/hr. Effects were examined with paired *t*-tests.

BEHAVIOR	CONTROL		TREATMENT		PERCENT CHANGE	<i>t</i>	<i>P</i>
	GRAND \bar{x}	SE	GRAND \bar{x}	SE			
Frequency							
All perch behaviors							
Nest building/main- tenance	25.8	1.4	30.8	2.1	19.4	2.36	0.029
Incubate	9.9	0.9	7.2	0.8	-27.3	3.11	0.006
Brood	9.4	0.7	8.6	0.7	-8.5	1.43	0.169
Feed young	6.5	0.7	6.2	0.6	-6.2	0.62	0.544
Rest	3.9	0.4	3.7	0.5	-5.1	0.41	0.698
Response ^a	4.6	0.7	5.2	0.7	13.0	1.09	0.289
	0.01	0.01	8.0	1.8	>100	4.46	0.0003
Duration							
All perch behaviors	456.6 ^b	17.8	439.3	16.8	-3.9	0.99	0.333
Nest building/main- tenance	33.9	6.7	28.7	6.7	-15.3	0.71	0.484
Incubate	324.8	9.7	318.9	7.0	-1.8	1.19	0.247
Brood	223.2	21.0	178.7	22.4	-19.9	2.25	0.038
Feed young	26.8	3.3	33.0	5.6	23.1	0.95	0.355
Rest	108.9	20.0	103.0	17.4	-5.4	0.13	0.902
Response ^a	<0.001	<0.001	10.7	2.0	>100	5.31	<0.0001

^a Pooled disturbance responses included flushes, standing in alert posture before and after flushing, and flight (evasion, surveillance, or aggression) before eagles resumed pre-disturbance activity.
^b Behavior of both adults on each territory was pooled so duration of all perch behaviors exceeded 6 hr.

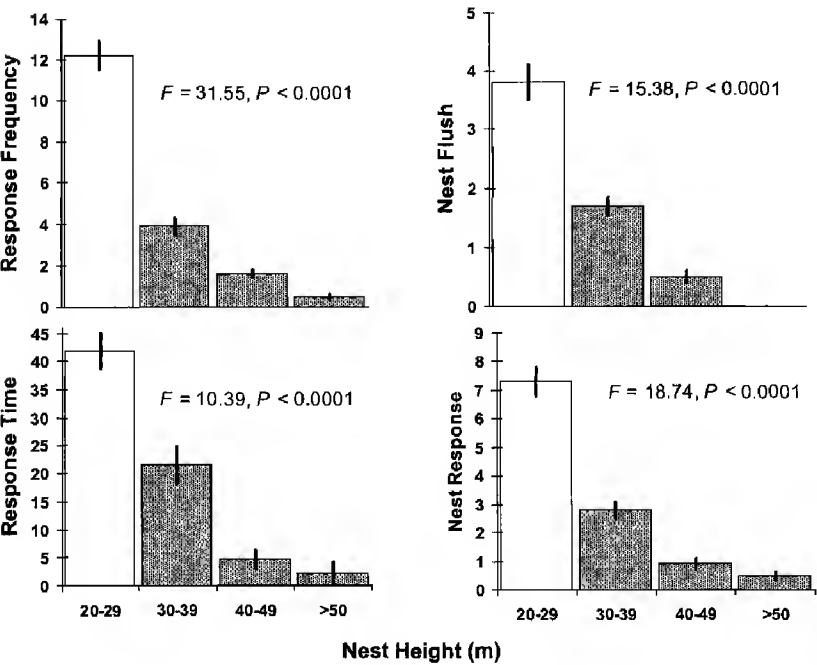


Figure 1. Effect of nest height on responses of Bald Eagles to experimental pedestrian activity at 21 nests in western Washington. Response rates (number of responses or min of response/hr of activity) were compared with the Bonferroni procedure. Responses included flushes, alert posture, and flight before eagles resumed previous activity. Means with different shading are statistically different (error bars = SE).

an intruding eagle. The remaining four encounters (5%) involved incubating or brooding adults engaged in physical aggression with an intruder on the nest, or leaving the eggs or young unattended while pursuing an intruding adult. Two encounters on the nest occurred during treatments.

Eagles did not habituate during six pedestrian exposures on a treatment day based on frequency ($P = 0.192$) or time ($P = 0.663$) of responses.

Effects of Nest Height, Screening, Distance, and Nesting Stage. No interactions were identified between the four factors on nine eagle behaviors ($P > 0.116$), but individual factor effects were significant. Nest height mitigated the effects of pedestrians near nests; four eagle responses were reduced at nests >29-m high (Fig. 1). Combined responses of eagles on the nest were reduced to <1/hr of pedestrian activity at nests >40-high, and eagles did not flush from nests >50-m high. Nest screening also ameliorated effects of pedestrian activity for three responses (Fig. 2). There was a mean decrease of three responses/hr between low and partially-screened nests, and a further reduc-

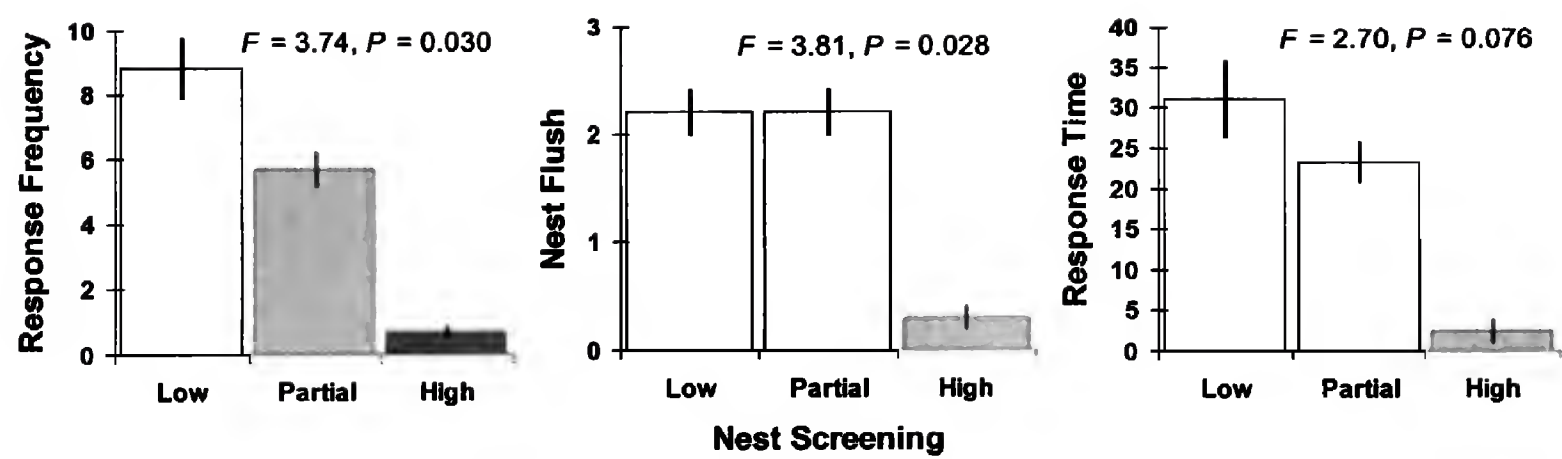


Figure 2. Effect of nest screening on responses of Bald Eagles to experimental pedestrian activity at 21 nests in western Washington. Response rates (number of responses or min of response/hr of activity) were compared with the Bonferroni procedure. Responses included flushes, alert posture, and flight before eagles resumed previous activity. Means with different shading are statistically different (error bars = SE).

tion of five responses/hr when nests were highly-screened. Highly-screened nests also significantly reduced eagle response time and nest flushes compared to other screening classes. Pedestrian distance to nests only affected eagle response time ($F_{8,56} = 4.01, P = 0.024$). Eagle response time at 30 m ($\bar{x} = 19.9 \pm 3.7$ min/hr of activity) was not significantly different from 60 m ($\bar{x} = 18.4 \pm 2.8$ min/hr of activity), but both were significantly greater than at 120 m ($\bar{x} = 11.9 \pm 4.4$ min/hr of activity). Nest stage only affected total responses ($F_{8,56} = 7.37, P = 0.009$). Eagles responded almost twice as often during the brood period ($\bar{x} = 6.5 \pm 1.4$ responses/hr of activity) compared to incubation ($\bar{x} = 3.3 \pm 0.7$ responses/hr of activity).

At given levels of screening and nest height the predicted eagle response frequency was reduced by a mean of 1.6/hr when pedestrian distance increased from 60–120 m (Table 3). At nests 20–29 m in height, response frequencies were reduced up to 18% at specific screening levels when distance increased from 60–120 m. At nests 30–39 m in height, response frequencies were reduced up to 33% at specific screening levels when distance

increased to 120 m. At nests >40 m in height, responses were reduced from 50–100% as pedestrian distance increased from 60–120 m.

DISCUSSION

Successful management of Bald Eagle habitat depends, in part, on identifying factors that affect eagle responses to human activity, and understanding how to manipulate those factors to reduce their impacts. This study illustrates that in non-pristine, forested environments, nest height, and vegetative screening are important factors for mitigating eagle responses to brief exposures of a single pedestrian. Height of nests in which eagle responses were reduced to insignificant levels (i.e., >40 m) was considerably less than average response distance to pedestrians (i.e., 72 m). This suggests that nest height affords eagles a more substantial buffer against disturbance than horizontal distance. Nest height was a significant predictor of call rates, dive rates, and minimum approach distances that Red-tailed Hawks exhibited toward an observer (Andersen 1990). Flushes from nests are potentially the most detrimental eagle response, and this re-

Table 3. Predicted reduction in mean frequency (95% Confidence Interval) of Bald Eagle responses per hr of pedestrian activity when distance to the nest is increased from 60–120 m (N = 21 nests).

NEST HEIGHT (m)	NEST SCREENING					
	LOW		PARTIAL		HIGH	
	60 m	120 m	60 m	120 m	60 m	120 m
20–29	11.5 (2.1)	9.9 (2.8)	10.2 (1.8)	8.6 (2.7)	8.9 (3.1)	7.3 (3.6)
30–39	7.4 (2.1)	5.8 (2.8)	6.1 (1.1)	4.5 (2.2)	4.8 (2.2)	3.2 (3.0)
>40	3.3 (2.8)	1.7 (3.3)	2.0 (1.6)	0.4 (2.4)	0.7 (2.0)	0.0 (0.9)

sponse was ameliorated only by nest height and vegetative screening. Screening had marked effects on the frequency of flush and flight responses for eagles both on and away from the nest. Earlier research found nesting eagles responded to human activity when the activity first became visible (Grubb et al. 1992, Steidl and Anthony 1996). Partial screening reduced response time by 32% compared to open nests, and in some situations appeared to allow just enough visibility of the pedestrian to alert the eagle, but prevent it from monitoring pedestrian activity, resulting in a flush. Seventy-two percent of surveillance flights, when eagles circled the nest site during and after treatments, involved situations with the nest partially screened.

Manipulation of encounter distance produced less dramatic changes in responses. Mean response distance (71 m) and flush response distance (72 m) of eagles I studied were similar to breeding eagles at 33 nests in western Washington that flushed in response to humans in nonexperimental settings at a mean distance of 86 m, and exhibited alert responses at 143 m (J. Watson unpubl. data). Similarly, camping <100 m from Bald Eagle nests affected eagle behavior, compared to >500 m away (Steidl and Anthony 2000). The distances that breeding eagles in Washington responded to pedestrians were less than has been documented in other studies in the United States (e.g., 185 m, Grubb et al. 1992; 275 m, Grubb and King 1991; 57–991 m, Fraser et al. 1985), possibly reflecting a higher degree of habituation to human activities by eagles in western Washington. Studies which evaluated six characteristics of Bald Eagle responses in Arizona and Michigan, found distance to be the most important characteristic of pedestrian disturbance, followed by duration or sound of activity, and then visibility (Grubb and King 1991, Grubb et al. 1992).

Nest stage affected eagle tolerance to pedestrian disturbance with brooding eagles responding twice as long, on average, than incubating eagles. For both periods most response time was spent passively perching following flushing, prior to resuming the previous activity. During incubation, eagles usually sat more tightly on nests, resulting in fewer responses while the pedestrian was present. After treatments, incubation resumed more quickly than did brooding. Bald Eagles exhibited the same differences in nesting responses to close helicopter approaches in northwest Washington (Watson

1993). Control comparisons for exposure of eggs (3 min) and young (57 min) showed eagles exhibited a natural decrease in tenacity to nests throughout nesting, which amplified the time they spent off nests in the brood period. Eaglets begin to thermoregulate at ca. 15 d (Bortolotti 1984) and require less brooding thereafter. Coincident increases in daytime temperatures and decreasing precipitation throughout nesting may have progressively reduced the need for parental attendance. Wetter and colder days in early spring corresponded to increased time on eggs and small young after exposures. Such compensation is important during incubation to reheat cooled eggs of nesting raptors, especially during frequent exposures between 30–60 min that lower egg temperatures to <35°C (Fox 1995). I found mean egg exposure times decreased 3 min/hr in the absence of pedestrian activity, with an additional reduction in exposure time of 3 min/hr on days with precipitation. Captive Bald Eagles reduced the length of time they left eggs exposed from ca. 2 min/hr to 0.6 min/hr at ambient temperatures <7.2°C and wind velocities >16.2 km/hr (Gerrard et al. 1979). Thus, Bald Eagles exhibit flexibility in their incubation strategies depending on human disturbance and weather conditions. This flexibility probably explains the unexpectedly long exposure times for eggs even on control days (e.g., maximum 110 min).

Among nesting pairs of Bald Eagles there is a wide range of tolerance to pedestrians that may result from certain pairs being more habituated to higher existing human-activity levels on their territories (McGarigal et al. 1991). Research on raptors and American Crows (*Corvus brachyrhynchos*) indicated that increased human interactions from urbanization influenced bird behavior in such a way that they have become more tolerant of human intrusion near nests (Newton 1979, Knight et al. 1987, Grubb et al. 1992). However, I did not find that eagles habituated to experimental activity during a treatment day. Steidl and Anthony (2000) found short-term (e.g., daily) habituation of eagles, but no long-term (e.g., weekly) habituation to human activity levels. Different tolerance limits of individuals may, in part, result from past experience and nestling imprinting (Newton 1979, Harmata 1984).

This study illustrated the potential for detrimental behavioral responses of Bald Eagles during brief exposures to human activity. Because intensity of

pedestrian activity during the study (10.0 min/hr for 6 hr) was in the range observed in typical circumstances in western Washington (J. Watson unpubl. data), I believe the results are representative of existing conditions. The need to reduce human activities that elicit eagle responses is based on the assumption that such efforts will increase survival and productivity (e.g., Fraser 1981, Grier and Fyfe 1987, Anthony and Isaacs 1989, Steidl and Anthony 2000). I did not detect damage or injury to eggs or young that occurred when adults were flushed from nests (Grier and Fyfe 1987, Yates and McClelland 1989); although nearly half of the eagles were on nests during pedestrian activity and flushes from nests constituted half of the responses. I observed no predation of eggs or young (Yates 1989), although exposure during two treatment episodes provided the opportunity for conspecifics to attack young, and for adults to incidentally harm them during violent agonistic encounters. A two-fold increase in mean egg exposure time increased the likelihood that eggs would be affected by cooling, overheating, or loss of moisture (Gerrard and Bortolotti 1988). A mean reduction in incubation time by 14 min/hr was related to nest failure at 40 Bald Eagle nests in western Washington (J. Watson unpubl. data).

MANAGEMENT RECOMMENDATIONS

Effects of pedestrian activity <120 m from nests on Bald Eagles with some previous exposure to human activities in non-pristine, rural environments can be reduced by regulating the distance of disturbance as a function of nest height and screening vegetation on a site specific basis (Table 3). Guidelines to promote reduced disturbance include maintaining and enhancing vegetative and topographic features that totally screen Bald Eagle nests from pedestrian activities. A high degree of screening, as opposed to partial screening, is particularly critical when pedestrian activity must be allowed ≤ 60 m from nests. Where partial screening exists, or is proposed by removal of vegetation on undeveloped property (e.g., creating "view windows" or limbing), maintaining some degree of screening vegetation is preferred to completely removing the cover, but will provide eagles substantially less protection from disturbance compared to dense cover. Planting trees or vegetation near exposed nests will not reduce responses of eagles in the short term unless they effectively conceal hu-

man activities from the nest, but should be encouraged to provide future nesting habitat.

Management plans should not reduce pedestrian restrictions based solely on nest tree height, because eagles will select new trees and build nests at different heights over time. On eagle territories with limited management options, maintaining an adequate number of trees >40 m tall may reduce the long-term impacts of reduced screening and closer human activities.

Timing conditions in Bald Eagle management plans should restrict pedestrian activities during incubation and the first 3 wk of brooding when adults exhibit similar flush rates and subject eggs and young to the possibility of being crushed or ejected from nests (e.g., second wk of February through the fourth wk in May for western Washington; J. Watson unpubl. data). Time away from eggs or small young would be more critical during inclement weather, in harsher climates, and at higher elevation sites. Restrictions during later brooding (4–5 wk) through fledging (e.g., 12 wk), a period not specifically addressed in this research, should address activities that may inhibit delivery of prey to young, potentially affecting their survival (Bortolotti 1989, Anthony et al. 1994, Steidl and Anthony 2000).

Outreach programs explaining Bald Eagle management should inform the public that untrained observers may greatly underestimate their disturbance of nesting Bald Eagles. Incubating and brooding eagles will respond roughly 30% of the time pedestrians are present <120 m from nests, and nearly 70% of the eagle response time will be spent perching passively, exposing eggs and young to the elements and predators. Because Bald Eagles nesting in pristine environments may exhibit greater sensitivity to pedestrians than those in this study, similar experiments should be conducted in those areas to evaluate distance and cover relationships before management conditions are implemented.

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DISPERSAL AND MORTALITY OF RED-SHOULDERED HAWKS BANDED IN OHIO

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ABSTRACT.—We banded nestling Red-shouldered Hawks (*Buteo lineatus*) in southwestern Ohio and northern Kentucky (SW OHIO, hereafter) to examine movements and determine causes of mortality in this suburban population. For comparison, we examined band recovery records for nestling Red-shouldered Hawks banded in rural northern Ohio. Of 899 nestlings banded in SW OHIO from 1955–2002, 43 (4.8%) were encountered (dead or alive) some time after fledging. Mean distance from natal nest at time of encounter was 38.5 ± 13.6 km and was not correlated with hawk age ($P > 0.58$). Distance from natal nest did not differ for hawks of three age classes or between those encountered in the breeding and nonbreeding seasons ($P > 0.13$). Cumulative exponential distribution (CED) analysis of distance from natal nest at time of encounter indicated that 50% of SW OHIO Red-shouldered Hawks were found <15 km from their natal nest, 75% were <29 km away, and 95% were <62 km away. Mean age of hawks recovered dead was 1.9 ± 0.4 yr ($N = 31$). CED analysis of age at recovery indicated that 50% of Red-shouldered Hawks were dead by age 1.2 yr, 75% by 2.4 yr, and 95% by 5.2 yr. SW OHIO hawks did not differ from hawks banded in northern Ohio in either distance from natal nest or age at recovery.

KEY WORDS: *Red-shouldered Hawk; Buteo lineatus; natal dispersal; survival; banding; urban.*

DISPERSION Y MORTALIDAD DE *BUTEO LINEATUS* ANILLADOS EN OHIO

RESUMEN.—Anillamos pichones de *Buteo lineatus* en el sudoeste de Ohio y norte de Kentucky (SO de Ohio, en adelante) para examinar los movimientos y determinar las causas de mortalidad en esta población suburbana. De modo comparativo, examinamos datos de anillos recuperados de pichones de *Buteo lineatus* anillados en áreas rurales del norte de Ohio. De 899 pichones anillados en el SO de Ohio entre 1955 y 2002, 43 (4.8%) fueron encontrados (muertos o vivos) algún tiempo después de abandonar el nido. La distancia al nido natal en el momento del encuentro fue de 38.5 ± 13.6 km y no estuvo correlacionada con la edad del ave ($P > 0.58$). La distancia al nido natal no difirió entre águilas de tres clases de edad ni entre aquellas encontradas en la estación reproductiva y no reproductiva ($P > 0.13$). Los análisis de la distribución exponencial acumulativa (DEA) de la distancia desde el nido natal en el momento del encuentro indicaron que el 50% de las águilas del SO de Ohio fueron encontradas

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a <15 km del nido natal, 75% a <29 km de distancia y 95% a <62 km de distancia. La edad media de las aves recobradas muertas fue de 1.9 ± 0.4 años ($N = 31$). Los análisis de DEA de la edad en el momento del encuentro indicaron que el 50% de los individuos ya habían muerto a una edad de 1.2 años, 75% a una edad de 2.4 años y 95% a una edad de 5.2 años. Las águilas del SO de OHIO no se diferenciaron de las anilladas en el norte de Ohio en la distancia desde el nido natal ni en la edad al momento de recuperación del anillo.

[Traducción del equipo editorial]

The breeding habitat of the Red-shouldered Hawk (*Buteo lineatus*) in some areas of North America has been described as remote (Johnson 1989, Bosakowski et al. 1992, Bosakowski and Smith 1997). However, the species also inhabits suburban areas, at least in California (Bloom and McCrary 1996, Rottenborn 2000) and in southwestern Ohio near Cincinnati (Dykstra et al. 2000, 2001a, 2003). In southwestern Ohio, Red-shouldered Hawks built nests a mean of 75 m from human residences (Dykstra et al. 2000), and their 90-ha home ranges contained a mean of 169 residences each (Dykstra et al. 2001b). Two pairs of southwestern Ohio Red-shouldered Hawks have nested on rooftops and one pair on a gas grill on the deck of a residence (Hays 2000, Dykstra et al. 2001b).

Suburban-nesting raptors may experience different threats than those encountered by their rural-nesting conspecifics (Love and Bird 2000). They may endure repeated human disturbance (Preston and Beane 1996) and risk of collision with vehicles and buildings (e.g., Peregrine Falcons [*Falco peregrinus*]; Sweeney et al. 1997). They also may face a higher risk of other kinds of human-induced mortality, such as electrocution on power lines (e.g., Harris's Hawks [*Parabuteo unicinctus*]; Dawson and Mannan 1995) and persecution.

Although suburban areas can provide significant breeding habitat for species facing habitat loss in more traditional natural and rural settings, suburban areas also are subject to rapid development that may displace even the most tolerant raptor species. The continual conversion of forested areas to lawn and other nonnative vegetation may reduce prey populations to levels inadequate to sustain raptor populations, even if suitable nest sites are available. As urbanization proceeds and habitat deteriorates, fledglings able to disperse long distances from their natal nest may have the best opportunity to locate suitable breeding habitat. Fledglings of species with short natal dispersals may be less likely to find adequate breeding sites, which eventually may result in regional population decline.

We banded nestling Red-shouldered Hawks in southwestern Ohio to examine natal dispersal and determine causes of mortality in this suburban population. For comparison, we obtained band-recovery records from the Bird Banding Lab for nestlings banded in rural areas of northern Ohio. We anticipated that suburban hawks from southwestern Ohio and northern Kentucky have longer natal-dispersal distances than rural hawks because the fragmented-habitat mosaic of the suburbs might result in suitable nesting habitat interspersed among highly-developed, unsuitable space.

STUDY AREA

We banded nestling Red-shouldered Hawks in southwestern Ohio and northern Kentucky (SW OHIO, hereafter), in Hamilton, Clermont, and southwestern Warren Counties, OH, and northern Boone and Kenton Counties, KY, <27 km south of the Ohio-Kentucky border. Most nests at which nestlings were banded occurred in a wide band of suburban development and semirural areas surrounding the city of Cincinnati.

SW OHIO is a hilly, unglaciated area in the Interior Plateau ecoregion (Omernik 1987). The hills are dissected by many small streams located in ravines and by two large rivers, the Great Miami and the Little Miami. Native forests are dominated by second-growth oak-hickory (*Quercus* spp.-*Carya* spp.) and beech-maple (*Fagus grandifolia*-*Acer saccharum*) associations, with lowland-riparian forests characterized by sycamores (*Platanus occidentalis*) and beech. Suburban areas in SW OHIO varied from densely populated (residential lots ca. 20 × 35 m) to sparsely populated (>2.5-ha residential lots, as well as undeveloped private land). Most residences and other buildings were surrounded by lawns and other nonnative vegetation, but residences tended to be located on level ground, with steep slopes and riparian areas left in native vegetation. Public land within the study area consisted primarily of native vegetation, with some developed areas for sports and other recreational uses.

METHODS

Banding. Red-shouldered Hawk nestlings in SW OHIO were banded with U.S. Fish and Wildlife Service (USFWS)/ U.S. Geological Survey (USGS) bands between 1955–59, 1963–77, and 1996–2002. Most nestlings banded between May 1998 and June 2002 were also banded with colored-plastic bands (Haggie Engraving, Crumpton, MD U.S.A.) inscribed with individual alpha-numeric codes large enough to be observed from the ground with

binoculars or a spotting scope. Nestlings were banded at ca. age 2–5 wk.

Band Recoveries and Encounters. We defined a band recovery as a report of a hawk that had died, and a band encounter as any report of a banded hawk, dead or alive. Most reports were further investigated by contacting the individual who had reported the band.

We also encountered color-marked hawks in the course of other fieldwork. Color bands were read with a spotting scope or binoculars, or the marked bird was captured using a bal-chatri trap baited with a mouse (Bloom 1987). Other banded birds ($N = 2$) encountered by birders were reported directly to the bander. Four banded birds that were injured were brought to RAPTOR, Inc., a local rehabilitation organization. Additional bands recovered in nests or on the ground under nests were not included in this study.

We determined causes of death for recovered birds from USGS Bird Banding Laboratory (BBL) records (“How obtained” codes) or by carcass examination. We determined gender of dead hawks, when possible, by examination ($N = 4$), and gender of live hawks by behavior (i.e., copulation observed) or the presence/absence of a brood patch ($N = 5$).

For comparison, we obtained from the BBL reports of band recoveries and encounters for birds banded at various rural locations in northern Ohio ($>40^\circ\text{N}$ latitude) by seven banders. The birds represented were banded from 1940–72.

Data Analyses. Banding locations in SW OHIO were defined by street addresses in most cases ($N = 37$) and plotted on USGS 7.5' topographic maps. Encounter locations in SW OHIO were defined by street addresses in most cases ($N = 27$) or by the nearest town as indicated on the BBL “Report to the bander” data card ($N = 9$). Specific location data were lacking for some older banding locations ($N = 6$), encounters ($N = 7$), and for all banding and encounter locations in northern Ohio, so we designated these locations as the center of the 10-minute block indicated in BBL records.

To estimate age of hawks at the time of the encounter, we assumed that all nestlings hatched on 23 April, the mean hatch date for SW OHIO 1997–99. We classified encounters into three categories based on age at the time of encounter: <298 d, 298–663 d, and >663 d. Birds <298 d were those encountered before 15 February in the year following the year in which they were banded, and thus, were not breeding birds. We selected 15 February as a cut-off date because by that date most birds in SW OHIO had begun breeding activities, such as territory occupancy and nest-building (Dykstra et al. 2000, 2001a). Birds 298–663 d were those encountered between 15 February of the year following that in which they were banded and the subsequent 15 February, and thus, were in immature plumage and possibly breeding. Birds >663 d were those in mature plumage and were probably breeding birds. We also classified encounters according to the season in which they occurred. We considered 15 February–31 July to be the breeding season (Dykstra et al. 2001b), and 1 August–14 February the nonbreeding season.

Although Red-shouldered Hawks normally begin breeding in their third spring at 2 yr, they may breed first

as immature-plumaged yearlings in their second spring (Wiley 1975, Crocoll 1994). Natal dispersal has been defined as the movement from birthplace to the site of the first breeding attempt (Greenwood 1980, Greenwood and Harvey 1982). However, because adult Red-shouldered Hawks in SW OHIO apparently are year-round residents (Dykstra et al. 2001a, 2001b), any bird encountered at age >663 d or older was likely located at or very near its breeding site, regardless of the season. For simplicity, we assumed this location to be the first breeding site. Thus our measure of natal dispersal included all birds >663 d encountered in any season, as well as yearling birds known to be breeders.

Results are shown as mean \pm 1 standard error of mean. Because of skewed distributions, the distance from natal nest and age at encounter data were log-transformed before statistical analysis. We used t -tests, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) to test for differences in distance from natal nest, and linear regression to examine the relationship between distance from natal nest and age at encounter.

We examined age at recovery using cumulative exponential distribution (CED) following Harmata et al. (2001) and Harmata (2002). Age in years (x) of each recovered hawk from SW OHIO was listed in order from youngest to oldest and the cumulative proportion of recoveries calculated for each. For the purposes of calculation, the proportion of 1.0 was expressed as 0.9999999. We fitted cumulative proportion of recoveries by age to the CED function $y = 1 - e^{-bx}$. The predicted proportion of recoveries (y) generated from this function were used in the transformed function $bx = \ln(1 - y)$. The $\ln(1 - y)$ was calculated and regressed with the observed x (with zero intercept) to determine the coefficient (β) of age variable x . We also examined distance from natal nest at time of encounter using CED analysis following Harmata et al. (2001).

RESULTS

Band Encounter Rate and Circumstances of Encounters. Of 899 nestling Red-shouldered Hawks banded in SW OHIO from 1955–2002, 43 (4.8%) were encountered some time after fledging and before January 2004. Of 28 SW OHIO hawks that were recovered, 14 (50%) were simply “found dead,” five (18%) were hit by vehicles, four (14%) were electrocuted, two (7%) were found injured and later died, and one each (4%) were caught in a trap, shot, and found as a band with bone or skeleton only. Three other bands were returned; we assumed these hawks were dead and thus included them with the recoveries. Twelve hawks were encountered alive: nine (75%) of these were color-marked birds that we sighted or trapped in 1999–January 2004, one (8%) was hand-caught during a storm and released, one was trapped by a bander, and one was obtained without information.

Table 1. Movements of Red-shouldered Hawks banded as nestlings in southwestern Ohio and northern Ohio, and encountered after fledging.

BANDING REGION	AGE AT ENCOUNTER	N	DISTANCE FROM NATAL NEST (km)		
			MEAN \pm 1 SE	MEDIAN	RANGE
Southwestern Ohio	<298 d	14	68.5 \pm 36.5	13.7	3.9–500.0
	298–663 d	11	33.6 \pm 23.4	8.5	0.0–266.1
	>663 d	18	18.2 \pm 5.4	11.8	0.8–103.2
	Total	43	38.5 \pm 13.6	12.3	0.0–500.0
Northern Ohio ^a	<298 d	11	38.4 \pm 13.6	18.5	0.0–145.3
	298–663 d	2	40.4 \pm 17.2	40.4	23.2–57.6
	>663 d	10	92.6 \pm 58.7	28.0	0.0–612.9
	Total	23	62.1 \pm 26.2	27.9	0.0–612.9

^a From USGS Bird Banding Laboratory records, banded 1940–72.



Figure 1. Map of long-distance (>100 km) dispersal of Red-shouldered Hawks banded as nestlings in southwestern OH, 1955–2002. Lines join natal sites and encounter locations. All birds shown were recovered dead and four of the five birds shown were <663-d old at recovery.

Distance from Natal Nest. For SW OHIO birds, mean distance from natal nest at time of encounter was 38.5 ± 13.6 km (Table 1). Most birds moved <30 km, but five birds were recovered 103–500 km from their natal nest (Fig. 1). CED analysis of distance from natal nest at time of encounter indicated that 50% of SW OHIO Red-shouldered Hawks were found <15 km from their natal nest, 75% were <29 km away, and 95% were <62 km away ($R^2 = 0.98$, $\beta = -0.048$, $P < 0.001$, $N = 43$; Fig. 2). Natal dispersal averaged 18.2 ± 4.9 km, $N = 20$ (males 9.3 ± 2.6 km, $N = 4$; females 16.5 ± 4.7 km, $N = 5$, 11 sex undetermined). One bird was recovered 103 km from its natal nest; the other 19 were encountered <30 km from their natal nests ($\bar{x} = 13.7 \pm 2.0$ km).

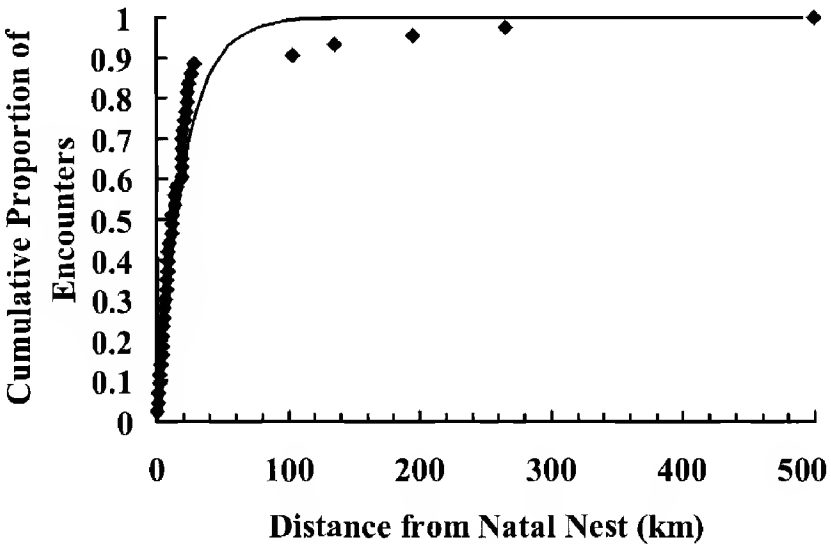


Figure 2. Cumulative exponential distribution of distance from natal area for Red-shouldered Hawks banded as nestlings in southwestern OH and northern KY, 1955–2002.

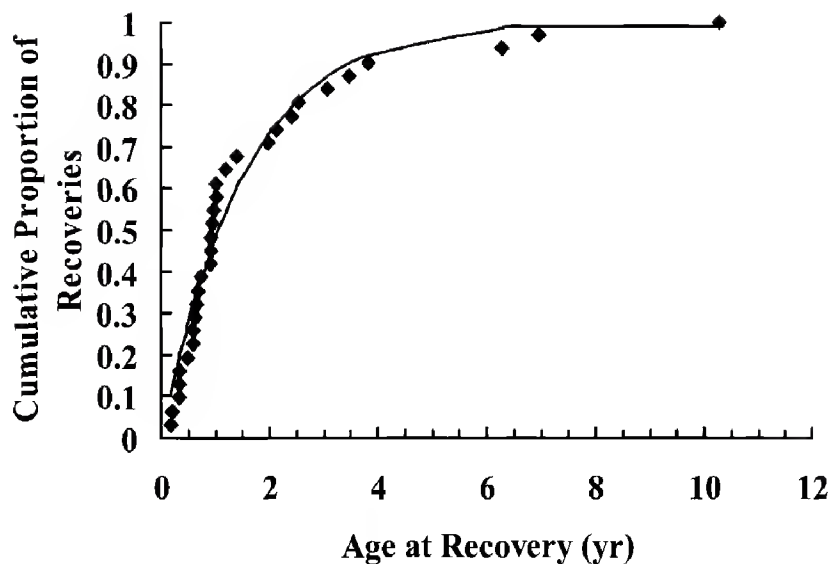


Figure 3. Cumulative exponential distribution of age at recovery for Red-shouldered Hawks banded as nestlings in southwestern OH and northern KY, 1955–2002.

Distance from the natal nest differed between birds recovered dead and those encountered alive ($t = 2.455$, $df = 41$, $P = 0.018$), so the two categories were tested both separately and combined for analyses below; the combined results are presented when there were no differences. Distance from natal nest was not correlated with age at encounter ($P > 0.58$), and did not differ among age classes ($P > 0.18$). Birds encountered during the breeding season were neither nearer nor farther from their natal nests than birds encountered during the nonbreeding season ($P > 0.13$, $N = 24$ for breeding season, $N = 19$ for nonbreeding season).

When compared to BBL records for birds banded as nestlings in rural northern Ohio, those banded in SW OHIO moved slightly shorter distances (Table 1), but there were no differences in distance from natal nest for all age classes combined or for birds <298 d or those >663 d ($P > 0.250$; Table 1). Among rural-northern Ohio birds alone, the distance from the natal nest did not differ between birds encountered in the breeding and nonbreeding seasons ($P > 0.583$); however, when adjusted for age class, there was a tendency for birds to be farther from the natal nest during the nonbreeding season than during the breeding season (ANCOVA, age class as covariate, $F = 3.719$, $P = 0.068$, $R^2 = 0.17$, $N = 23$).

Age at Recovery. Mean age at recovery for Red-shouldered Hawks banded in SW OHIO was 1.9 ± 0.4 yr ($N = 31$ hawks). CED analysis indicated that 50% of Red-shouldered Hawks were dead by age 1.2 yr, 75% by age 2.4 yr, and 95% by age 5.2 yr ($R^2 = 0.96$, $P < 0.001$, $\beta = -0.577$; Fig. 3).

SW OHIO birds did not differ from northern Ohio birds in age at recovery ($t = 0.038$, $df = 51$, $P = 0.97$). For northern Ohio birds alone, the mean age at recovery was 2.0 ± 0.4 yr ($N = 22$). CED analysis indicated that 50% of northern Ohio Red-shouldered Hawks were dead by age 1.1 yr, 75% by age 2.3 yr, and 95% by age 4.9 yr ($R^2 = 0.93$, $P < 0.001$, $\beta = -0.607$, $N = 22$).

DISCUSSION

Dispersal from the Natal Nest. Mean dispersal distance was 38.5 km, with 50% of the hawks found <15 km from their natal nest. Natal-dispersal distance, the distance from birthplace to a breeding site, was 18.2 ± 4.9 km. Similarly, Red-shouldered Hawks in other parts of their breeding range also have short natal-dispersal distances. In Wisconsin, 11 banded nestlings that were recaptured as breeding birds had dispersed a mean of 17 km from their natal site (Jacobs and Jacobs 2002). Jacobs and Jacobs (2002) also determined from BBL data that $>54\%$ of 99 eastern Red-shouldered Hawks recovered in the breeding season were <30 km from their natal site.

In our study, birds encountered while alive, primarily color-banded birds we sighted or captured, had significantly shorter dispersal distances than those recovered dead. The inclusion of birds encountered alive may have caused the mean dispersal distance to be underestimated because we did not search for color-marked birds outside the study area. Also, birds were more likely to be encountered within the heavily-populated suburban region surrounding Cincinnati than in rural regions outside the study area. Underestimation of dispersal distance is not uncommon in dispersal studies because long-distance dispersers are less likely to be detected than short-distance dispersers (Koenig et al. 1996). Nonetheless, within the study area, we believe that local-dispersal distances were likely correct because, despite ca. equal effort in banding and trapping throughout the study area, we found only two birds that moved as far as the distance from the west side of the study area to the east side, a span of 30–50 km.

We anticipated that young birds <663 d might be encountered farther from their natal nest than those of breeding age (>663 -d old), because young raptors of some species tend to move far from the natal nest after they gain independence and before they begin breeding (Walls and Kenward 1998, Forero et al. 2002, Byholm et al. 2003).

Although we did not find significant differences in encounter distance for birds of different ages, we did note that four of the five birds found at long distances from their natal nest were <2-yr old, suggesting that young Red-shouldered Hawks might also wander.

Although not significant statistically, mean dispersal distance for SW OHIO was slightly smaller than for rural northern Ohio hawks (Table 1). This difference might reflect true differences between suburban and rural birds, or it may have resulted from an ecological difference between the two populations. Our age-adjusted analysis indicated that northern Ohio birds encountered in the nonbreeding season tended to be farther from their natal nest than those encountered in the breeding season, suggesting that some northern birds migrate. A more comparable rural population that is likely nonmigratory is located in southeastern Ohio; in this population, we banded 217 nestlings from 1997–2002, but recovered only two bands (0.9%, C. Dykstra and J. Hays unpubl. data).

Mortality. Most mortality for Red-shouldered Hawks in SW OHIO occurred within the first 14 mo of life, as it did for northern Ohio birds. Henny (1972) examined band-recovery data for Red-shouldered Hawks in six regions of North America and determined mortality rate for the first year of life to be 0.58. High first-year mortality is typical of raptors (Newton 1979). The oldest Red-shouldered Hawk recovered in this study was over 10 yr 3 mo old, but Jacobs and Jacobs (2002) report several hawks that were at least 10–14 yr old and one 17 yr old. The oldest wild Red-shouldered Hawk recorded was 19 yr 11 mo (Clapp et al. 1982).

Most SW OHIO hawks died of unknown causes, but of those for whom cause of death was known, 38% were killed by motor vehicles and an additional 31% by electrocution on power lines or electric fences. Although sample sizes are small, these data suggest that interactions with humans and human-made structures may be an important agent of mortality for urban/suburban raptors. Similarly, for urban Harris's Hawks in Tucson, at least 72% of mortality in which cause could be determined was due to electrocution (Dawson and Mannan 1995). Among midwestern Peregrine Falcons, a primarily urban population, 81% of injured falcons admitted to the Raptor Center at University of Minnesota had sustained injuries from collisions with vehicles, buildings or utility lines (Sweeney et al. 1997). Mortality of urban adult Lesser Kestrels (*Fal-*

co naumanni) in southern Spain was ascribed to collision with vehicles (13% of mortalities with known cause), persecution by humans (25%), electrocution (8%), and entanglement in safety nets erected for building restoration work (21%), for a total of 67% of mortality due to interaction with humans (Tella et al. 1996). In contrast, in a species with a typically rural distribution, Red-tailed Hawks (*Buteo jamaicensis*), only 32% of mortalities with known causes were due to collisions with vehicles, electrocution, and gunshot wounds, while the majority were due to poisonings by agricultural pesticides (19%), emaciation (25%), and disease (16%; Franson et al. 1996).

Dispersal and Urbanization. The short natal-dispersal distances for Red-shouldered Hawks, combined with the increasing urbanization of the Cincinnati area and its suburbs, may make it increasingly difficult for young Red-shouldered Hawks fledged in SW OHIO to find suitable breeding habitat. Currently, this suburban population does not appear to be compromised in any way. Compared to more rural populations in Ohio and elsewhere, the SW OHIO birds reproduced well at a fairly high nest density, found suitable nest sites (Dykstra et al. 2000), and maintained home ranges that were typical in size for Red-shouldered Hawks (Dykstra et al. 2001b), although they were less forested than those measured elsewhere (Howell and Chapman 1997). However, anecdotal evidence suggests that hawks may be losing nesting habitat as urbanization proceeds: in a sample of 22 nesting territories, where hawks were banded in 1963–77, only 10 of them still contained nesting hawks by 1997–98 (Dykstra et al. 2000).

Red-shouldered Hawks of SW OHIO may be able to maintain their population if they are able to further adapt to humans and suburban landscapes. Red-shouldered Hawks in southern California may be even more adjusted to urban conditions than those in Ohio; nesting urban birds there tolerated large crowds attending athletic events as well as people camping directly underneath their nest trees (Bloom and McCrary 1996). A few individual hawks in SW OHIO may be similarly tolerant, as evidenced by the two nests located on rooftops and one located on a suburban deck (Hays 2000, Dykstra et al. 2001b). In summary, the suburban Red-shouldered Hawk population of SW OHIO is apparently well-adapted to humans, although it remains uncertain whether these suburban birds

will be able to maintain their numbers in the face of further urbanization and suburban sprawl.

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DECREASES IN A POPULATION OF RED-SHOULDERED HAWKS NESTING IN CENTRAL MARYLAND

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ABSTRACT.—I report the results of a 32-yr (1971–2002) nesting study of the Red-shouldered Hawk (*Buteo lineatus*) in central Maryland that adds 31 yr of observations to an earlier long-term study. Regression analysis indicated that from 1975–2002 the number of nesting pairs in the study area decreased by at least 78%. An estimate of the population change based on the number of successful nests (fledging at least one young) indicated a decrease of about 88%. The number of young fledged/successful nest decreased slightly. Modest downward trends in the numbers of Red-shouldered Hawks observed during the local Christmas Bird Counts since 1972 provide further evidence of a population in decline. These long-term trends in this nesting population's size and nesting success were contrary to patterns expected as the density of hawks decreased. Human activities resulting, both directly and indirectly, in habitat changes detrimental to this species were likely the principal reasons for these local decreases; similar to declines observed in other Red-shouldered Hawk populations.

KEY WORDS: *Red-shouldered Hawk*; *Buteo lineatus*; *central Maryland*; *breeding success*; *population decline*.

DISMINUCIONES EN UNA POBLACIÓN NIDIFICANTE DE *BUTEO LINEATUS* EN EL CENTRO DE MARYLAND

RESUMEN.—En este trabajo documento los resultados de un estudio de 32 años de duración (1971–2002) sobre la nidificación de *Buteo lineatus* en el centro de Maryland, añadiendo 31 años de observaciones a un estudio previo de largo plazo. Análisis de regresión indicaron que el número de parejas nidificantes en el área de estudio disminuyó por lo menos en un 78% entre 1975 y 2002. Otro estimado del cambio poblacional basado en el número de nidos exitosos (con al menos un pichón emplumado) indicó una disminución de alrededor del 88%. El número de pichones emplumados por nido exitoso disminuyó ligeramente. Las tendencias moderadas de disminución en el número de *B. lineatus* observados durante los conteos navideños desde 1972 proveen evidencia adicional de que la población está en disminución. Estas tendencias de largo plazo en el tamaño de esta población nidificante y en su éxito de nidificación fueron contrarias a los patrones esperados con la disminución de la densidad poblacional. Las actividades humanas que llevan directa o indirectamente a cambios nocivos en el hábitat para esta especie fueron probablemente las razones principales que explican estas disminuciones locales, de forma similar a las disminuciones observadas en otras poblaciones de *B. lineatus*.

[Traducción del equipo editorial]

In the spring of 1947, U.S. Fish and Wildlife Service biologist Robert Stewart (1949) led a nesting study of the Red-shouldered Hawk (*Buteo lineatus*) in the Patuxent River watershed in parts of Prince George's and Anne Arundel counties, MD covering the coastal plain from Laurel and Fort Meade to tidewater. That study, which included records dating back to 1943, reported a variety of information on the Red-shouldered Hawk (hereafter RSHA) including habitat requirements, population densities, reproductive performance, and food habits. From 1960 through 1967 Fred Schmid, an-

other biologist at the Patuxent Wildlife Research Center (PWRC), located nests and banded nestlings in the heart of Stewart's study area. His observations are included in Henny et al. (1973). In late 1970, a group of biologists led by Charles Henny designed a follow-up study on a portion of Stewart's original area to determine this species' status, a study centered on but not limited to the PWRC. I, with many volunteers, have continued to monitor this RSHA population to provide a continuous 32-yr record using the same methods to extend earlier observations. Because many birds and other species are known to decline in abundance as their habitat patches decrease in size and quality, such

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long-term monitoring is especially useful in this area of growing urbanization as the PWRC area becomes an increasingly isolated large patch of forest. Henny et al. (1973) noted that the PWRC remained an atypical "island of remaining habitat," where the RSHA population still seemed to be doing well at a time when many other populations of this species were declining. Bednarz and Dinsmore (1981) cited 14 references indicating that the RSHA population had declined in Iowa and elsewhere and was listed as rare or endangered in five states, probably largely due, directly or indirectly, to habitat change. These authors stated that "Timber harvesting (selective or clear-cutting), dam construction, and channelization all have major detrimental impacts on natural bottomland communities. Clearly, the Red-shouldered Hawk will continue to decline as river systems and lowland habitats continue to be modified and developed" citing several additional references to support this prediction. Titus et al. (1989) reported that five northeastern states had listed the RSHA as either "threatened," of "special concern," or a candidate for listing.

Data reported here supplement the earlier population data for central Maryland and enable me to test the hypothesis that the PWRC is still an island of prime RSHA habitat. I will thus examine the size and breeding success of the RSHA population on and around this area to learn if changes have occurred therein since the early 1970s and suggest possible causes for any changes.

STUDY AREA AND METHODS

The study area, as described by Henny et al. (1973), included a mostly mature woodland in the floodplain and adjacent upland along the Patuxent River from Laurel (39°06'07"N, 76°50'22"W) downstream to Bowie State University (39°02'04"N, 76°45'06"W). Since 1972, I have continued to cover this same area plus a 23% extension downstream to the old Bowie Race Track (39°00'36"N, 76°44'11"W), a total of about 1077 ha. Henny et al. (1973) also provided a detailed description of their methods and a thorough analysis of the population data available for the PWRC segment for the 29-yr period 1943–71. Even more detailed information on the area's physical characteristics together with annotated lists of much of the flora (Hotchkiss and Stewart 1947) and fauna of the PWRC were published in one booklet (Anonymous 1979). Following the methods of Henny et al. (1973), the study area was searched on foot from early March through May each year for any evidence of RSHA nesting ranging from courtship and nest building through fledging. Total nests found showing evidence of use by nesting RSHA (e.g., presence of an adult, fresh leafy material or down on the nest, droppings indicative

of young in the nest, and young seen in the nest) provided an index of population size each season. Any such nest from which at least one young most likely fledged (usually indicated by the number of young banded at >2.5 wk old, but including a few nests observed to have fledged unbanded young) is further defined as a *successful* nest. Generally nest trees were not climbed until time of banding, but nests that appeared unsuccessful were checked sooner, and several nests were visited at periodic intervals from the time of hatching to fledging. At these nests wing chord measurements were taken on several young every few days to provide information on growth rate and corresponding age in days. By taking the same measurements of the young in other nests when I banded them, I was usually able to estimate hatching dates within a few days.

In 1981, a fairly typical year in terms of study effort, about 110 hr were spent searching the area and an additional 50 hr returning to check the status of nests found, band the young, and record details on nests and young. I was able to get out mostly after work and on weekends, and thus, covered only a small portion of the study area each period in the field. As with any field work, some years had more days with adverse weather or trees leafed out earlier, while in other years, conditions for conducting this type of work were better. Thus, coverage of the area varied from year to year. However, I believe that over such a long period of data collection, sampling effort fluctuated around an average which was not biased relative to the changes I observed in this RSHA population. On the other hand, I suggest that my ability to identify and include unsuccessful nests and find a greater proportion of the total population likely improved with experience.

Each year, I found or was told about RSHA nests in central Maryland outside my study area. Also, in 1975 and 1976, I spent quite a bit of time searching for nests in several nearby areas. Data for nests located outside the study area are labeled as "other nests" and included in only those analyses which would not be affected by the tendency for this subsample to include more successful nests. Collection and contaminant analysis of a small sample of eggs (Henny et al. 1973) that failed to hatch continued into the mid 1970s.

I used the linear-regression program provided by Lotus 123, Release 5, (IBM Software Group, Cambridge, MA U.S.A.) primarily to assess changes over time; levels of apparent statistical significance (Snedecor and Cochran 1980) were included to emphasize patterns and the relative magnitude of suspected changes. I also examined local Christmas Bird Count (CBC) data using linear regression. I estimated percent change over the entire period by dividing the difference between the expected values provided by linear regression for the first and last years by the value for the first year. I used 2-tailed statistical tests for this analysis.

RESULTS

Despite increasing search efforts over the years, the number of RSHA nests found in my study area has decreased substantially each 10–12-yr period (Table 1). Also, nest success has declined from the

Table 1. Summary of Red-shouldered Hawk population status and nesting performance and changes therein in central MD, 1971–2002. Other nests are those outside of the defined study area (see Study Area and Methods) in central Maryland.

YEARS	LOCATION	NUMBER OF NESTS FOUND ^a	SUCCESSFUL NESTS		TOTAL YOUNG FLEDGED ^b	YOUNG PER		ESTIMATED HATCHING DATE OF OLDEST NESTLING		
			NUMBER	PERCENT		NEST FOUND	SUCCESSFUL NEST	EARLIEST	LATEST	MEAN
Period totals and means:										
1971-80	Study area	286 + 3?	199	69.6	470	1.64	2.36			
	Other nests	40	32	80.0	76	1.90	2.38			
	All nests	326 + 3?	231	70.9	546	1.67	2.36	10 Apr	2 Jun	28 Apr
1981-90	Study area	237 + 2?	138	58.2	311	1.31	2.25			
	Other nests	51	38	74.5	98	1.92	2.58			
	All nests	288 + 2?	176	61.1	409	1.42	2.32	5 Apr	30 May	29 Apr
1991-2002	Study area	144 + 1?	69	47.9	155	1.08	2.25			
	Other nests	57	38	66.7	89	1.56	2.34			
	All nests	201 + 1?	107	53.2	244	1.21	2.28	7 Apr	23 May	26 Apr
32-yr totals and means:										
1971-2002	Study area	667 + 6?	406	60.9	936	1.40	2.31			
	Other nests	148	108	73.0	263	1.78	2.44			
	All nests	815 + 6?	514	63.1	1199 ^c	1.47	2.33	5 Apr	2 Jun	28 Apr

^a Number with question mark indicates additional nests with fate not determined.
^b Totals do not include seven young fostered into observed nests from other areas.
^c Of 1125 nestlings banded through 2001, 27 (2.4%) were reported later, 21 dead and six alive.

Table 2. Results of linear regression analysis of key population parameters on Red-shouldered Hawks (RSHA) in central MD.

PARAMETER REGRESSION EQUATION	TOTAL CHANGE	PROBABILITY ^a
Number of nests found in study area ^b :		
Y value for 1971–2002 = 33.0 – 0.721x	–69.3%	<0.001
Y value for 1975–2002 = 34.9 – 0.984x	–78.3%	<0.001
Number of successful nests found in study area:		
Y value for 1972–2002 = 23.5 – 0.672x	–88.2%	<0.001
Percent successful ^b :		
Y value (1971–2002) = 70.8 – 0.765x	–33.9%	0.030
Y value (1975–2002) = 68.8 – 0.823x	–32.7%	0.030
Young/nest found ^b (1971–2002) = 1.70 – 0.023x	–42.8%	0.020
Young/successful nest (1971–2002) = 2.38 – 0.009x	–11.6%	0.180
Mean hatching date (1973–2002) = 27.7 – 0.050x	–5.2%	>0.500
RSHA/party-hr from BCBC (1972–2002) = 0.16 – 0.002x	–23.1%	0.030

^a Probability that slope (estimated change) is zero.
^b Estimates based on all nests found may be biased because the proportion of unsuccessful nests not found was not uniform throughout the study period.

first decade of study (69.6%) relative to the most recent period of monitoring (47.9%; Table 1). Statistically significant decreases are indicated both for nests found and for nesting success (Table 2). The number of nests found in the study area decreased by 69.3% since 1971 and by 78.3% since 1975. The number of successful nests (fledging young) has decreased by 88.2% since 1972 (Table 2). Because a smaller area was studied in 1971 and my skill at finding nests, especially unsuccessful nests, likely improved for the first several years, I consider the 1972–2002 estimate (–88.2%) based only on successful nests, the best measure of the population decrease. For the same reason, the percentage of nests successful and the number of young fledged/nest found (Table 2) were likely overestimates, especially early in the study. On the other hand, young fledged *per successful nest*, which should also be relatively unbiased, has shown little long-term decrease (Tables 1 and 2). Similar results were evident among the nests found outside my study area (Table 1). Mean hatching date (28 April) may have changed slightly (to 26 April; Table 1) since about the mid 1980s, but this pattern was not statistically significant (Table 2).

DISCUSSION

Based on the difficulties of finding unsuccessful nests, as noted above (also see Johnson and Shaffer 1990), I suggest my data pertaining to successful nests are more reliable than that on total nests

found, and I emphasize it here. With this subsample, there was a slightly sharper downward trend indicated in the numbers of successful nests found compared to all nests found (Table 2). Because successful RSHA nests tend to be more visible over a longer period than unsuccessful nests, they have a higher probability of being discovered by an observer than unsuccessful nests, especially those that fail early in the season. With experience, I feel I have become better at finding and identifying such unsuccessful nests and included an increasing proportion of them in my sample as the study progressed. However, nesting RSHAs often continue to occupy a territory again the following year, especially after a successful nesting season, tending to nest near the old nest site or even reuse the same nest. This makes nests in territories with a history of success easier to find year after year, and the likelihood of finding a higher portion of the successful nests thus increases as years go by. Overall, however, I believe the improvement in my ability to find unsuccessful nests had the greatest influence on my results. This more complete sample of unsuccessful nests at least partly explains the sharper decrease in young/nest found compared to young/successful nest (Table 2). However, finding more of the unsuccessful nests (and successful nests as well) should have caused total nests found in my sample to increase if the population was actually stable or increasing. Thus, as my population

figures must be more complete now than in the early years of the study, the population decrease may be even steeper than my data indicate. Also, although more people become aware of this study as years go by, fewer reports of nesting hawks now come to me from other observers; another indication that the RSHA nesting population has decreased in central Maryland.

Henny et al. (1973) looked at population density and nesting success on the PWRC from 1960–71 by comparing four years with up to six RSHA nests found and five years with more than six nests located. He found that young fledged/nest was 31% lower when there were more nests, which seemed to support a density-dependent response. However, young fledged/successful nest was only 12% lower. From 1971–2002, I had 15 years (most before 1984), in which nine or more nests were found. These sites had a mean of 2.19 young fledged/successful nest and 1.12 young fledged/nest found. I had 17 years, mostly since 1983, with eight or fewer nests located, from which 2.12 young fledged/successful nest (–3%), and 1.27 young fledged/nest found (+15%). If the data back to 1960 are included, there were 25 years with fewer than nine nests found, which produced 2.15 young fledged/successful nest (–2%), and 1.32 young fledged/nest found (+18%). These data do not support the occurrence of density-dependent responses in reproductive success. However, the question of whether or not the unsuccessful nests were included in the proper proportion, especially in the early years, remains. Thus, I consider the figures based on successful nests to be the most reliable.

During the early years of this research, I assumed I was seeing normal annual fluctuations in the size and reproductive success of a relatively stable breeding population. I considered differences from year to year to be due to variations in weather conditions and other natural variables. Henny et al. (1973) concluded that rainfall had no influence on the number of young fledged/nest found. However, their figures show the difference in young/successful nest to be somewhat larger and success higher when there were 1–2 d with at least 19 mm of rain during the nesting period compared to no rain. Their study did not include any years with a longer period of heavy rain. At least short-term fluctuations in the numbers of nesting pairs and their success may be related to larger weather changes. For example, in 1995, both young

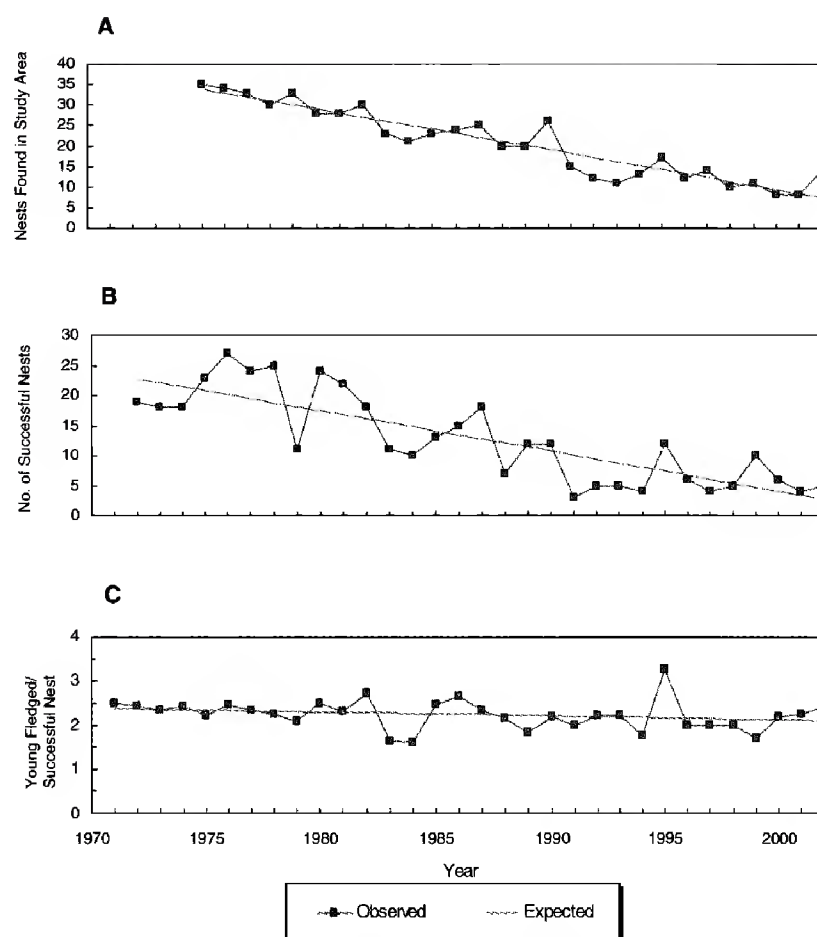


Figure 1. Trends shown in selected measurements of a Red-shouldered Hawk population in a central MD study area: (A) number of nests found from 1975–2002 ($r^2 = 0.88$, $b = -0.98$), (B) number of successful nests found from 1972–2002 ($r^2 = 0.67$, $b = -0.67$), and (C) number of young fledged/successful nest from 1971–2002 ($r^2 = 0.06$, $b = -0.009$).

fledged/successful nest (Fig. 1) and young fledged/nest found were the highest recorded in this study, an exception to the general long-term trend. This unusually successful nesting season was preceded by milder and drier than normal winter and early spring weather and followed several years of markedly colder, wetter weather with lower nesting success (Fig. 1). Generally, local weather conditions appear to me to have continued to fluctuate normally while the nesting RSHA population has declined to new lows (Table 1), a decrease which seems to have been largely independent of local weather conditions. However, changes in weather cannot be entirely ruled out. After a review of over 2000 published papers, the IPCC (Gittay et al. 2002) published an overview of the effects of climate changes, especially global warming, on biodiversity around the world. Among their findings: “There has been a discernible impact of regional climate change, particularly increases in temperature, on biological systems in the 20th century.” They go on to say “Such systems include, for

example . . . species distributions, and population sizes." They point out that such climate changes may impact different species in a community in different ways. For example, by putting the timing of breeding out of synchrony with the times when food is available to prepare adults for breeding or later to feed their young.

Development-related activities, particularly construction of buildings, roads, and power lines around the edges of and in the study area accompanying a growing human population, have caused a gradual deterioration in and even destruction of at least some RSHA bottomland habitat in the PWRC area as it has in many other areas (e.g., Bednarz and Dinsmore 1981, Bryant 1986). Motor-bike trails now run through the bottomland in several areas. Near Laurel in an area where "paintball wars" were conducted, I found two paintballs resting in an unsuccessful RSHA nest. Also, an expanding beaver (*Castor canadensis*) population has resulted in flooding of numerous lowland sites and the cutting and drowning of many trees and other vegetation. In addition, early in this study some logging occurred in and near the bottomland in the downstream portion of the study area. I have not attempted to measure the habitat loss, but there does not yet appear to me to be any shortage of nest sites or food for hawks in the study area, though the size and quality of many RSHA territories has likely been changed for the worse. The changes seen in the RSHA population provide the best indication of this decline in habitat. While some authors (e.g., Howell and Chapman 1997) suggest that openings such as those made by logging and beaver in woodlands benefit RSHAs, others (e.g., Bednarz and Dinsmore 1982, Moorman and Chapman 1996) found that the Red-tailed Hawk (*Buteo jamaicensis*) tended to replace RSHAs when a floodplain was opened up and fragmented. Bryant (1986), aware of widespread concerns for the status of the RSHA, studied a local population in Ontario and concluded that selective logging there had created habitat more attractive to the Red-tailed Hawk (hereafter RTHA), which forced out the RSHAs previously nesting there. I have observed increased nesting by, competition with, and predation on RSHAs in my study area by Great Horned Owls (*Bubo virginianus*) and RTHAs which now find this area better suited to their habitat requirements. The impact of Great Horned Owls was especially evident in 2000, when the remains of at least four adult RSHAs were found, three in or

near their nests and a fourth in a Great Horned Owl nest. Signs of such losses have become an annual event, and I consider this as evidence that the decrease in this RSHA population was the result, both directly and indirectly, of the habitat changes observed.

While acknowledging comparison with recruitment standards (Henny 1972) that "may be slightly biased high," Henny et al. (1973) concluded tentatively that the observed recruitment rate of 1.95 fledglings/breeding pair/yr with 77% of the nesting pairs successful on the PWRC appeared to be adequate for maintaining the population. However, for most of my study, both recruitment rate and percentage of pairs nesting successfully (Table 1) have been *well below* the means reported by Henny et al. (1973). Thus, I have concluded that my study area and nearby areas contained a RSHA population that was not stable between 1971–2002, but was in fact decreasing significantly. Henny et al. (1973) also concluded that "Therefore, it is doubtful that the relatively low pesticide levels in the eggs had a detrimental effect on the reproductive performance of the population." Eggs collected in this study later in the 1970s gave results similar to those shown in Henny et al. (1973) and continue to support that conclusion.

The Bowie Christmas Bird Count (BCBC), sponsored by the local chapter of the National Audubon Society, provides additional evidence that this RSHA population has decreased (Table 2). This count, in which I have been a regular participant, began in 1972 and includes nearly all my study area and a much larger nearby area (a Christmas count circle includes almost 45770 ha), encompassing many of my other nest sites. Regression analysis indicated that the BCBC RSHA count/party-hr has decreased by 23.1% since 1972 (Table 2).

Many, if not all, of the RSHAs in my study area are year-round residents as indicated by a radiotelemetry study of local adult RSHAs in the late 1980s by M. Fuller and his assistants (Senchak 1991) and by band-recovery information. Thus, both my breeding population data and the BCBC winter population data, the latter including local young-of-the-year, likely relate to the same resident population, and both provided evidence of a population decrease. In another analysis of CBC data, McKay et al. (2002) found a substantial decrease in the RSHA population in the 1960s and no sign of recovery to former levels in a portion of the Mississippi River valley in Iowa and Illinois. An ear-

lier study (Brown 1971) of CBC data from 1950–69, showed the RSHA population to have “decreased markedly” in a group of northern and eastern states, with a decrease of about 50% indicated for Maryland.

As discussed above, Henny et al. (1973) suggested that the nesting success of this RSHA population was density-dependent with pairs nesting closer to each other producing fewer young than pairs nesting farther apart. Thus, other factors being equal, a less dense population should have higher nesting success. However, in my study, both population density and nesting success showed decreases. In contrast, Rottenborn (2000) found both an increasing RSHA population and high nesting success in a study in California, crediting this to the unusual habitat, particularly *Eucalyptus* spp. and *Washingtonia* spp., introduced species, which increased nest site availability. Few, if any, other studies provide long-term data on both population levels and nesting success. It seems clear from my study that other factors may not be equal, that nesting success can be affected by more than just population density. Evidence of compensatory interaction between RSHA nesting success and nesting density, at least over three decades in central Maryland, appears to be lacking. On a broader scale, Henny (1972) compared mean numbers of young banded/successful nest, an estimator of young fledged/successful nest, during the periods 1900–45 (2.50 birds) and 1946–68 (2.33 birds) in a mid-Atlantic region centered on Maryland. The decrease of about 7% between these periods was not statistically significant. However, he found even larger decreases in the three other regions of the nation for which similar data were available suggesting that widespread decreases in nesting success had occurred between the early 1900s and 1968. During this period, the continental RSHA population was also believed to have undergone a widespread decline (e.g., Henny 1972, Bednarz and Dinsmore 1981). Thus, these apparent decreases in both population size and nesting success were not confined to a few scattered study areas. Again, support for the operation of density dependence and compensatory interaction appears to be lacking, at least under conditions of declining habitat quality and quantity.

RSHA populations in many other areas seem to have been decreasing at least through the 1960s. The relatively stable population apparent here until at least the early 1970s was viewed by Henny et

al. (1973) as a local phenomenon—a population in an “island of remaining habitat.” An analysis by Bednarz et al. (1990) suggested that the numbers of RSHA counted at Hawk Mountain, PA declined significantly between 1946–86, consistent with decreases in all five northeastern Breeding Bird Survey (BBS) strata. I do not expect the PWRC RSHA population to continue to decline in a straight line as assumed by linear regressions. Rather, I propose this population may be beginning to stabilize at a lower level as suggested by recent patterns in my data (Fig. 1).

A number of authors including Bednarz and Dinsmore (1981) and Bryant (1986) have presented evidence and argued that widespread habitat changes in recent years could be expected to produce relatively large-scale decreases in the RSHA population. This appears to have happened in my study area and in at least some other areas. However, this evidence of relatively widespread RSHA population decreases through at least the 1990s seems to be contradicted by data from the North American BBS that indicated for the period 1966–99 that the RSHA population increased in the U.S. by a mean of 2.5%/yr. This change was statistically significant, but one to be viewed with caution for a variety of sampling and biological reasons (Pardieck and Sauer 2001). Analysis for the 1966–2002 period (Sauer et al. 2003) gives a similar result at the U.S. level and indicates a 4.8% increase for Maryland (almost reaching statistical significance) for the 1972–2002 period. Could deterioration of RSHA habitats leading to lower populations have forced the remaining birds to range over larger, more open territories to survive, making them more conspicuous along BBS routes? Because of low detection rates, the BBS is likely a less perfect technique for measuring most raptor populations than it is for measuring most other bird populations. Or, as I speculate above, perhaps the RSHA population is beginning to stabilize at a relatively low level or even to recover in some areas.

More work is needed to resolve these contrary indications from different data sets. Continuation of RSHA population monitoring here together with broader studies here and elsewhere should shed further light on causes and patterns of RSHA population change. Particular attention should be given to habitat modification and destruction, but also to some perhaps less obvious threats. While the RSHA was apparently among the species relatively unaffected by DDT during or after the period

of its use, 1946–72 in most areas (Bednarz et al. 1990), other environmental contaminants may be a factor. Also, the threat of West Nile virus (*Flavivirus* sp.) to the RSHA population needs to be examined.

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I will not attempt to list the many people who assisted with various phases of this study from locating nests through banding nestlings as it would take much space and some would undoubtedly be overlooked; however, their help was essential and was much appreciated. I am especially indebted to C.S. Houston who kindly read several of my early annual updates on this study, provided much editorial help, and urged me to publish my data, and to G. Allen, J.C. Bednarz, C.R. Dykstra, C.S. Robbins, J.R. Sauer, and several anonymous reviewers who also provided many helpful editorial suggestions and comments on various versions of this paper.

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SEASONAL VARIATION IN SEX RATIO OF NESTLING ELEONORA'S FALCONS¹

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ABSTRACT.—In a breeding colony of Eleonora's Falcon (*Falco eleonora*) on an island offshore of Crete, we determined the gender of 95% of the chicks by molecular (PCR) methods; 1028 samples were collected between 1997–2001. Hatching occurred between 11 August and 12 September with a variation of up to 5 d between years. The overall sex ratio was biased toward male fledglings (52.1%). The percent of males was positively related to the time of hatching. Falcons that hatched during the first 10 d of the hatching period had a higher daughter to son ratio. We propose that such bias may be adaptive because males with a higher fitness start to breed earlier and invest preferentially in female offspring than in lighter males. This hypothesis could explain some of the discrepancies in earlier sex-ratio studies on other raptors.

KEY WORDS: *Eleonora's Falcon; Falco eleonora; molecular sexing; sex allocation; sex ratio; male fitness.*

VARIACIÓN ESTACIONAL EN EL COCIENTE DE SEXOS EN PICHONES DE *FALCO ELEONORAE*

RESUMEN.—En una colonia reproductiva de halcones *Falco eleonora* en una isla cercana a la costa de Creta, determinamos el género del 95% de los pichones por medio de métodos moleculares (PCR) empleando 1028 muestras colectadas entre 1997–2001. La eclosión se produjo entre el 11 de agosto y el 12 de septiembre con una variación de hasta 5 días entre los años. El cociente de sexos global estuvo sesgado hacia volantes machos (52.1%). El porcentaje de los machos estuvo positivamente relacionado con el momento de la eclosión. Los halcones que eclosionaron durante los primeros 10 días del período de eclosión tuvieron un cociente mayor de hijas a hijos. Proponemos que este sesgo podría ser adaptativo ya que los machos con una adecuación mayor comienzan a reproducirse más temprano e invierten preferentemente en crías hembras que en machos más livianos. Esta hipótesis podría explicar algunas de las discrepancias observadas en estudios previos del cociente de sexos en otras rapaces.

[Traducción del equipo editorial]

The reason why primary and secondary sex ratios in raptors and other birds can deviate from parity has been widely debated (Bennet and Owens 2002, Hardy 2002, Komdeur and Pen 2002). Because it is often difficult to monitor a large number of nests within a single season, some studies suffer from small sample size. Several studies are biased toward species with a pronounced gender size dimorphism because this gender difference was formerly used to sex fledglings. As a consequence, de-

viations from parity tended to be discussed in relation to body size, the main explanations focusing on the advantage for female nestlings in food competition with male nestlings or on the advantage for males because of their smaller size and lower food requirements. Several obstacles which limited the selection of study species and timing of such studies have been overcome with the introduction of molecular techniques for gender determination (Ellegren and Sheldon 1997).

We selected Eleonora's Falcon (*Falco eleonora*) for a sex-ratio study because this species breeds in colonies with broods of 1–3 nestlings, so that a sufficiently large sample size could be obtained. In spite of its colonial habits, this falcon is monoga-

¹ This contribution represents part 28 of a series on Eleonora's Falcon.

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mous (Swatschek et al. 1993). Furthermore, egg laying starts at the end of July during the stable weather conditions of the Mediterranean summer so that breeding performance rarely differs between years (Walter 1979, Wink et al. 1985, Wink and Ristow 2000). This falcon is insectivorous during the courtship period when it feeds upon unpredictable food patches far away from the breeding cliff, but is mainly an avian predator during the brood-rearing period in September, when it feeds upon autumn-migrant passerine captured over the sea. Typically, half of the falcon population is 7 yr and older, and males begin to breed at 3 yr of age (Ristow et al. 1989).

METHODS

Field Work. Eleonora's Falcon is a species of conservation concern and included in Annex 1 of the European Union's Wild Bird Directive. Thus, to avoid disturbances caused by measuring eggs or trapping adults, we restricted our sampling to the period when the young are older than 10 d. Under natural conditions, egg losses are fairly high and nestling mortality comparatively low.

We studied a colony of about 150 falcon pairs on an island off Crete (<1 km² in size) between 1997–2001. Nests were visited once as a rule in mid-September. In ca. 20% of situations young were too small for measurement at the first visit, and these nests were revisited a second time about two weeks later. Thus, more than 95% of the fledglings of the colony were banded annually, their wing chord measured, and blood samples of ca. 50 µl each were taken and stored in DNA buffer (EDTA buffer) in a vial.

For both genders, wing chord was converted into hatching date by means of the growth curve formula

$$A = \frac{WC + 52.1}{9.71} \quad \text{for } 45 < WC < 113 \quad \text{and}$$

$$A = \frac{WC - 8.3}{6.16} \quad \text{for } 113 < WC < 242$$

in which WC is the wing chord in mm and A is the age of a nestling in days. The accuracy of this formula is ± 1 d (Wink et al. 1991). In some nests with three young, the third bird may experience extended periods of lower growth rate than its older siblings. In such cases the application of the growth formula would give an age difference in excess of 5 d between second and third nestling, a value which would exceed the maximum difference between egg laying dates (Wink et al. 1985); differences between hatching dates should be smaller or equal to this value in our population (Wink et al. 1991). In such cases (ca. 2% of cases) simply a 5-d age difference was assumed for the runt young. A calculated age difference of up to 7 d was accepted in nests with two young if an unhatched egg explained the gap (ca. 1% of cases).

DNA Isolation. Blood samples were preserved in an EDTA buffer (0.1 M Tris, pH 7.4, 10% EDTA, 1% NaF, 0.1% thymol; Wink 1998) and stored at -20°C until processing. Total DNA was extracted from the blood samples

by an overnight incubation at 37°C in lysis buffer (10 mM Tris [pH 7.5], 25 mM EDTA, 75 mM NaCl, 1% SDS) including 1 mg of Proteinase K (Merck, Darmstadt, Germany), followed by a standard phenol-chloroform protein extraction. DNA was precipitated from the supernatant with 0.8 volume of cold isopropanol, centrifuged, washed, dried, and resuspended in TE buffer (10 mM Tris-Cl, pH 7.5; 1 mM EDTA).

Molecular Sexing. Molecular sexing was modified (Becker and Wink 2002) according to the methods outlined in Kahn et al. (1998), which are based on the detection of the CHD gene on avian sex chromosomes. In most species, males produce one DNA band and females two, presumably reflecting differing intron sizes of the W versus Z chromosomes (Kahn et al. 1998). Polymerase chain reaction (PCR) used were 1237L: GAG AAA CTG TGC AAA ACA G and 1272H: TCC AGA ATA TCT TCT GCT CC. PCR conditions: the PCR mix consisted of 60 ng (2 µl) total DNA in 25 µl total volume, 0.12 µl 1272H Primer (97.45 pmol/µl), 0.103 µl 1237L Primer (83.1 pmol/µl), 1 µl nucleotide-mix (100 µM of GTP, CTP, TTP, and ATP), 2.5 µl 10× buffer with 15 mM MgCl, 0.15 µl Taq-Polymerase (0.6 Units; Pharmacia Biotech, Freiburg, Germany), and 0.1 µl ³³P α-dATP (1 µCi). PCR program: 2 min at 94°C , 31 cycles with 30 sec at 94°C , 1 min at 56°C , 2 min at 72°C , and finally 10 min at 72°C .

After 32 cycles the reaction temperature was maintained at 72°C for 4 min and then lowered to 4°C for further storage. PCR products were separated electrophoretically on a denaturing Sequagel matrix at 65 W for 1.5 hr (length 40 cm). After drying, the gel was exposed to an X-ray film (Hyperfilm-MP, Amersham, Freiburg, Germany), for 1–2 d, and developed (X-ray developer and fixer, Kodak, New Haven, CT U.S.A.).

RESULTS

The gender of 1028 young falcons from 556 nests was determined by molecular sexing (Table 1). As the number of infertile eggs and premature deaths amount to about 10% and <2%, respectively (Ristow and Wink 1985, Ristow et al. 1989, Wink et al. 1991), our data mostly reflect the primary sex ratio. There was a tendency to a higher percentage of sons as compared to daughters when all broods were considered (52.1% compared to the expected frequency of 50%; chi-square test, $P < 0.1$).

The mean hatching date varied by 5 d between years (Table 2). If the data are corrected for year-to-year variation by setting the first hatching date as day 1, a positive correlation ($r = 0.685$; $N = 24$; $P < 0.001$) was detected between the sex-ratio and the date of hatching. Daughters were more abundant during the first 10 d of the hatching period, whereas sons dominated in the middle and final period (Fig. 1).

Table 2. Yearly variation of hatching dates of sons and daughters, and the percentage of males in Eleonora's Falcon broods (Crete, Greece, 1997–2001). The median hatch dates are used to characterize the center of the asymmetrical yearly distributions.

YEAR	MEDIAN FOR SONS	MEDIAN FOR DAUGHTERS	DIFFERENCE	PERCENTAGE OF MALES
1997	23.5	22.3	1.2	53.0
1998	25.7	24.3	1.4	49.8
1999	28.5	27.0	1.5	50.5
2000	26.0	25.6	0.4	54.3
2001	22.8	21.7	1.1	53.5
Total	24.4	23.5	0.9	52.1

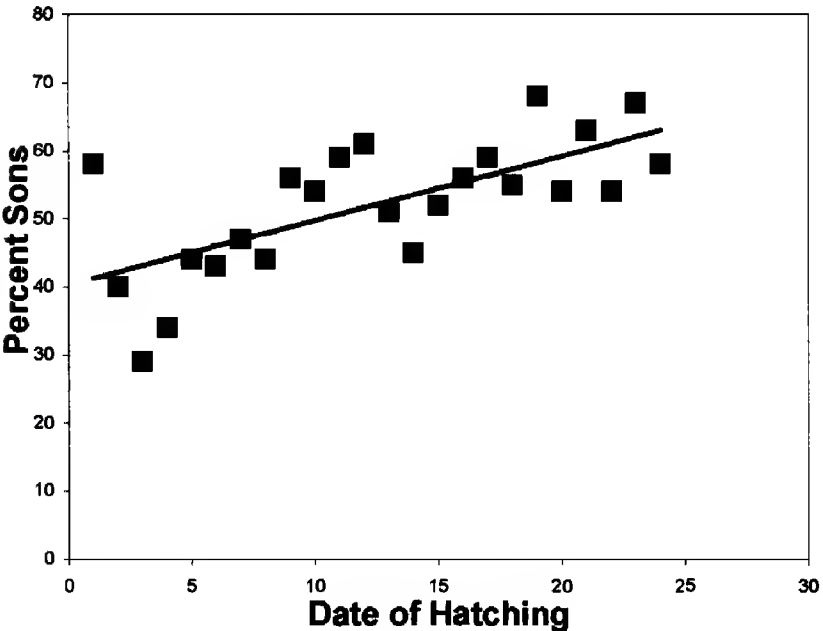
DISCUSSION

This study was carried out during a period of population decline caused by poisoning of falcons on mainland Crete resulting with instant death of many adults (Ristow 2001, Anonymous 2002); thus, the number of nestlings sampled decreased from 234–187 between 1997–2001 (Table 1). We assume that this effect was not responsible for the observed gender bias, which was present within each year (Table 2). Nor did we find evidence of a gen-

der bias in embryo mortality, although our data from unhatched eggs are few (3 males, 3 females).

We interpret the early bias toward daughters in the first third of the hatching period to reflect to some degree the fitness of parents and of males in particular. From previous studies on fitness in Eleonora's Falcon, Wink et al. (1985) established that large and heavy males have larger clutches and that mass between partners was uncorrelated. Mass of males (and likely fitness) increases with age, three-egg clutches tend to be started earlier in the breeding period than smaller clutches, and the first egg laid is the heaviest within a clutch (Wink et al. 1982a, 1985, 1991). The sum of these details was that experienced and successful pairs tended to start clutches early, and these produced more daughters. Vice versa, light males apparently produce more sons. In the case of Eleonora's Falcon, our results may be interpreted that the heaviest (fittest) males can afford to invest into the rarer gender, which needs a larger food supply (daughters were 15–20% heavier than sons; Wink et al. 1982b, 1991). This interpretation is in line with the observation that 11 pairs had three daughters each as compared to only seven pairs with three sons each.

Figure 1. Seasonal variation of sex ratio in Eleonora's Falcons ($N = 1028$ fledglings, Crete, Greece, 1997–2001). The Y-axis indicates mean daily percentage of males and the X-axis standardized days of hatching. The following standardization procedure was adopted: 13 August was set as day 1 for 1997 as the first year; the distributions of the following years in Table 1 were shifted by 2, 5, 3, and 0 d, respectively toward earlier dates (Table 2). Then, all broods earlier than day 1 were pooled with those of day 1. Similarly, 5 September was set as day 24 in 1997 and all later broods were pooled with those of day 24. Regression equation: $Y = 0.94x + 40.33$; $r^2 = 0.469$, $P < 0.001$.



If the above interpretation is valid, then the age of the adult males should be taken into account when comparing sex ratios among species. For example, no skewed sex allocation was found in Peregrine Falcons (*Falco peregrinus*; Burnham et al. 2003) in North America. The reevaluation of a study with German peregrines (data from Fig. 62 and Table 31, Rockenbach 2002) also did not reveal a statistically significant trend in sex ratios. These data sets were obtained in populations that were recovering after severe declines in the 1960s and 1970s and which consisted of a large percent-

age of young pairs. This might explain why in Australia, where such a decline had not taken place, a female-biased sex ratio was reported (Olsen and Cockburn 1991).

In Eurasian Kestrels (*Falco tinnunculus*) the proportion of sons increased with later laying in years of low and moderate food supply, whereas in years of good food supply the sex ratio was son biased throughout (Korpimäki et al. 2000). In this Finnish study of typically 30 falcon pairs, the population turn-over was >75% per yr, so that young breeders dominated. Also, in years of good food supply kestrels of inferior fitness could reproduce without chick loss. We suggest that this pattern is similar to what we observed for Eleonora's Falcons, in that less-fit males seemed to breed later in the season and produced male-biased broods.

In the American Kestrel (*Falco sparverius*), no trend or the opposite seasonal trend in the sex ratio of fledglings was reported (Anderson et al. 1997, Smallwood and Smallwood, 1998, Griggio et al. 2002). A simple explanation for this deviation from the other falcon species was not evident to us, but the extended laying season of 4 mo and the fact that males of this small falcon breed at 1 yr of age may be of relevance. Also in Lesser Kestrels (*Falco naumanni*) a secondary sex-ratio bias toward daughters as the breeding season progressed has been reported (Tella et al. 1996). Information about parents' age distribution would have helped to integrate these differing results into our suggested broader concept for falcons.

After having discussed the available data on falcon species that agree with or do not agree with our interpretation, it is worthwhile to examine data for other raptor species. Age of parents had been considered in the sex allocation of the Eurasian Sparrowhawk (*Accipiter nisus*; Risch and Brinkhof 2002), and these results were consistent with our interpretation of the Eleonora's Falcon data. However, neither parents' age nor fitness can explain the mechanism of how birds skew their offsprings' sex ratio. This becomes obvious when non-raptors are considered. For example, Cory's Shearwater (*Calonectris diomedea*) nesting on the same study island showed the opposite seasonal trend in sex ratio as compared to the Eleonora's Falcon (D. Ristow and M. Wink unpubl. data).

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TAWNY FISH-OWL PREDATION AT FISH FARMS IN TAIWAN

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ABSTRACT.—We examined the conflict between cold-water fish farmers and endangered Tawny Fish-Owls (*Ketupa flavipes*) in Taiwan. From 1994–2000, we surveyed 144 fish farms to assess the level of fish predation by Tawny Fish-Owls and to document farmers' responses to owl predation. From July 1994–May 1996, studies were conducted at five farms on Nanshih Stream in northern Taiwan and Tachia Stream in central Taiwan to determine the size of fish taken by the owls and the factors affecting predation rates. Owl predation was reported at 25 (17.4%) of the fish farms. Most farmers claimed that owl predation was most frequent during winter, then spring, fall, and summer. At 16 of these farms, owls were trapped with steel leg-hold traps or mist nets, and 10 owls were found drowned or floating in the fish ponds of eight farms. At the five intensively-studied fish farms, the owls took 8–131 (0.04–0.66%) of ca. 20 000 fish available each year. As the water level in streams increased, owls visited fish farms more often than expected. Owls foraged more frequently on clear nights and caught 101–400 g of fish more often than expected.

KEY WORDS: *Tawny Fish-Owl*; *Ketupa flavipes*; *fish predation*; *mortality*; *fish farms*; *Taiwan*.

DEPREDACIÓN DE PECES EN GRANJAS POR PARTE DE *KETUPA FLAVIPES* EN TAIWAN

RESUMEN.—En este estudio examinamos el conflicto entre los cultivadores de peces de agua fría y la especie de búho amenazada *Ketupa flavipes* en Taiwan. Entre 1994 y 2000, estudiamos 144 granjas de peces para establecer el nivel de depredación de peces por parte de *K. flavipes* y para documentar la respuesta de los cultivadores ante la depredación por parte de estas aves. Entre julio de 1994 y mayo de 1996, se realizaron estudios en cinco granjas en el arroyo Nanshih en el norte de Taiwan y el arroyo Tachia en el centro del país para determinar el tamaño de los peces consumidos por *K. flavipes* y los factores determinantes de las tasas de depredación. Se reportó depredación por parte de esta especie en 25 (17.4%) cultivos de peces. La mayoría de los cultivadores dijeron que la frecuencia de depredación era máxima durante el invierno y seguidamente menor en la primavera, el otoño y el verano. En 16 de estas granjas se capturaron búhos con trampas de acero o redes de niebla y 10 individuos fueron encontrados ahogados o flotando en los lagos de ocho cultivos. En las cinco granjas estudiadas intensivamente, los búhos capturaron entre 8 y 131 (0.04–0.66%) de los aproximadamente 20 000 peces disponibles anualmente. A medida que el nivel del agua en los arroyos se incrementó, las aves visitaron los cultivos de peces más frecuentemente que lo esperado. Los búhos forrajearon más frecuentemente en noches claras y capturaron 101–400 g de peces con mayor frecuencia que lo esperado.

[Traducción del equipo editorial]

Fish-owls are often regarded as nocturnal counterparts of the diurnal Osprey (*Pandion haliaetus*), fish eagles (*Ichthyophaga* spp.), and sea eagles (*Haliaeetus* spp.). Fish-owls include four species of *Ketupa* in Asia and three species of *Scotopelia* in Africa (Fogden 1973). The Tawny Fish-Owl (*K. flavipes*), the only fish-owl found in Taiwan, occurs from the Himalayan foothills of Kashmir and Garhwal, east

to the mountains of northern Laos, Vietnam, and south China, and north almost to the Yellow River (Voous 1988). In Taiwan, the Tawny Fish-Owl is rare, primarily due to the degradation of riparian habitat and illegal hunting (Severinghaus 1987). This species is listed as endangered under the 1989 "Wildlife Conservation Law" (Council of Agriculture 1989).

In Taiwan, cold-water fish farming in low-elevation mountain streams began in 1960–65 (Tzeng

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1988). Fish-owls prey upon farmed fish, including rainbow trout (*Oncorhynchus mykiss*) and ayu (*Plecoglossus altivelis*; Wang et al. 1994). Although protected, the owls have been illegally trapped or killed by farmers. While some farmers claim that owl predation causes major losses, to date no data have been presented to substantiate these claims.

Understanding the extent and cost of fish predation by owls is necessary to prioritize conservation activities and to implement effective management of this rare bird. In this study, we investigated Tawny Fish-Owl predation on farmed fish and the interactions between fish-owls and fish farmers.

STUDY AREA AND METHODS

We conducted this work in Taiwan. With an annual precipitation of 1000–6700 mm and an annual mean temperature of 22–24°C (Taiwan Forest Bureau 1995), about one half of the island is dominated by luxuriantly-forested mountains. Taiwan has ca. 129 streams, ranging from 10–200 km in length.

From the Taiwan Department of Fisheries database, we acquired information on 220 registered cold-water fish farms. We excluded farms in deforested suburban areas, where fish-owls do not reside (Sun 1996). The remaining 144 farms were located in the mountains in potential fish-owl habitat. From 1994–2000, the farmers of these farms were interviewed by questionnaire (with an owl picture) and by telephone. Questions included in the questionnaire simply asked whether farmers had seen this owl depredate fish or found fish scales and remains on walkways at their farms. Of the surveyed farms, 108 (75%) were located in central and northern Taiwan, where the climate is cooler and more suitable for cold-water fish farming, and 36 were located in southern Taiwan. We visited each farm that reported owl predation or found evidence of predation and asked farmers to rank the intensity of owl predation by season (spring: March–May, summer: June–August, fall: September–November, winter: December–February). Farmers provided a predation-intensity score from 1–4, which corresponded to owl predation that was very rare, rare, common, or very common, respectively. We also documented measures taken by farmers to protect fish from owl predation and the fate of owls trapped or taken by farmers.

From 1994–96, we closely examined Tawny Fish-Owl predation at four fish farms (two in each of two fish-owl territories) on Nanshih Stream (Sun et al. 2000) and at one fish farm in a fish-owl territory on Tachia Stream. Nanshih Stream ranges from 250–550 m above sea level, and is in northern Taiwan, 30 km south of Taipei. Three streams, Hawun, Chakung, and Talolan, join Nanshih Stream near Fusan, an aboriginal village. On the east and south banks of the stream, the vegetation consists mostly of subtropical rainforest dominated by *Ficus* and Lauraceae (Taiwan Forest Bureau 1995). Makino bamboo (*Phyllostachys makinoi*) and *Cryptomeria* (*Cryptomeria japonica*) plantations, farmland, and human habitations occupy much of the west and south banks. Tachia Stream is located in central Taiwan. It runs through warm-tem-

perate, montane forests of Lauraceae trees (Taiwan Forest Bureau 1995), *Cyclobalanopsis* sp., alder (*Alnus formosana*), Taiwan red pine (*Pinus taiwanensis*) and Taiwan short-leaf pine (*P. morrisonicola*). We documented fish predation by Tawny Fish-Owls at the Malin Fish Farm, 1000 m in elevation.

Each fish farm hatched 30 000–100 000 trout and ayu each year, mainly during January–March. Fish were kept in circular or rectangular fish ponds; each circular pond has an outlet in the center, unlike the rectangular one with an outlet located at the other side of the inlet. Trout grow to marketable size (>500 g) in 12–14 mo and ayu (80–120 g) take 5–7 mo. After harvest, 100–900 trout remained at each fish farm where they continued to grow (to 1500–2000 g) through the following year. These fish were sold or consumed at a later date. Unlike trout, ayu perished after breeding. Hence, farmed fish usually were available to owls throughout the year. At these five farms, we documented fish stocks, prey remains, the size (g), and species of fish taken by owls and the dates that owls caught fish. The size of fish taken by owls from ponds with fish of only one age class was easily estimated. For fish taken from ponds with fish of more than one age class, we estimated prey mass from sizes of the gills and scales in the remains. We were able to record the time of some predation events by opportunistic observations and radio-tracking. Owls were seen grabbing fish out of the water by their talons, holding them in talons on the bank, and sometimes plucking the gills and bladders out before swallowing pieces of meat.

We captured two Tawny Fish-Owls in each two territories by trapping them at night on tree branches or on pond banks at fish farms with foot-snare traps. The owls were then radio-tagged prior to release. Radio transmitters (MD-205; Telonics Inc., Mesa, AZ U.S.A.) weighed 70–80 g (< 3.5% of the owl's body mass) and had a lifespan of ca. 2 yr. Transmitters were attached dorsally with a backpack harness of wire (1.5 mm in diameter) wrapped inside a tubular teflon ribbon. Owls were located by homing a directional hand-held H-antenna with a TR-2 receiver (Telonics Inc., Mesa, AZ U.S.A.) and by triangulation, taking at least two bearings for each location.

We also examined whether owls more frequently preyed on fish in different stream flow conditions or during periods of different rainfall levels than expected. For each season and owl territory, the expected values were determined based on the proportion of the number of nights in different rainfall or stream flow categories during our observation period. The observed values were based on proportion of nights that we observed owl predation on farm fish during the different rainfall and stream-flow categories. We obtained rainfall (mm) data from the Taiwan Central Weather Bureau and water flow (m^3s^{-1}) data from the local hydrographic station of the Taiwan Power Company, which was <1 km from fish farms. Rainfall was categorized into two levels: 0–10 and >10 mm/d. Stream flow was classified as: low ($\leq 10 \text{ m}^3\text{s}^{-1}$), moderate (11–20 m^3s^{-1}) or high ($> 20 \text{ m}^3\text{s}^{-1}$).

Likewise, we examined whether owls preyed on fish in certain size classes more often than expected. For each owl territory, the availability of fish in each size class was estimated as the product of fish quantity ($\times 10^4$) and the

number of months the fish stayed in the pond. The proportion of fish in each size class taken by owls served as a measure of resource use.

Chi-square analysis (Conover 1980) was used to determine whether stream flow or rainfall was related to owl predation and to assess owl selection of fish by size. For significant relationships, analyses of selection (Bonferroni's *Z* test) described by Neu et al. (1974) were tested in terms of the use (observed) versus availability (expected) data. Differences in owl predation intensity among seasons were tested with the Friedman test (Conover 1980). Data were managed and analyzed with the Statistical Analysis System (SAS Institute 1989).

RESULTS

A total of 25 (17.4%) of the 144 fish farms reported owl predation. Two farms raised ayu, 18 had trout, and five farms raised both species. These farms were all from central and northern Taiwan, where most farms were located. Owl predation rates varied among seasons (Friedman, $\chi^2 = 17.0$, $P = 0.007$). Farmers claimed that owl predation was most frequent during winter (\bar{x} predation intensity score = 3.5, $N = 25$), than spring ($\bar{x} = 2.4$, $N = 25$), fall ($\bar{x} = 2.2$, $N = 25$), and summer ($\bar{x} = 1.9$, $N = 25$). However, at the two ayu farms (Nanao and Tungao) owl predation was highest during the summer (predation reported as very common, rank = 4).

After discovering fish remains on banks, farmers would set steel leg-hold traps or mist nets to catch the predator. Usually, it was only after the owl was captured that the farmers became aware of this rare owl species. Of the 25 fish farms reporting predation, Tawny Fish-Owls were caught at 16 fish farms from 1970–present. One owl was caught at 10 farms, nine farms caught two owls, and three farms caught three or more owls. Alarmingly, two farmers who had been in business for over 10 yr had caught more than five owls each. Farmers removed 28–37 owls that were caught in steel leg-hold traps and three in mist nets.

In addition, we recorded 10 incidents in which fishing owls were unable to get out of a pond at eight farms. Five owls drowned and five were alive and floating when they were found by farmers in the morning. Most accidents ($N = 8$) involved owls preying on large trout (600–900 g); an equal number of such incidents occurred in circular and rectangular fish ponds.

At the three Tawny Fish-Owl territories monitored, the seasonal pattern of owl predation was somewhat mixed (Fig. 1). Predation intensity generally increased in October or November and was

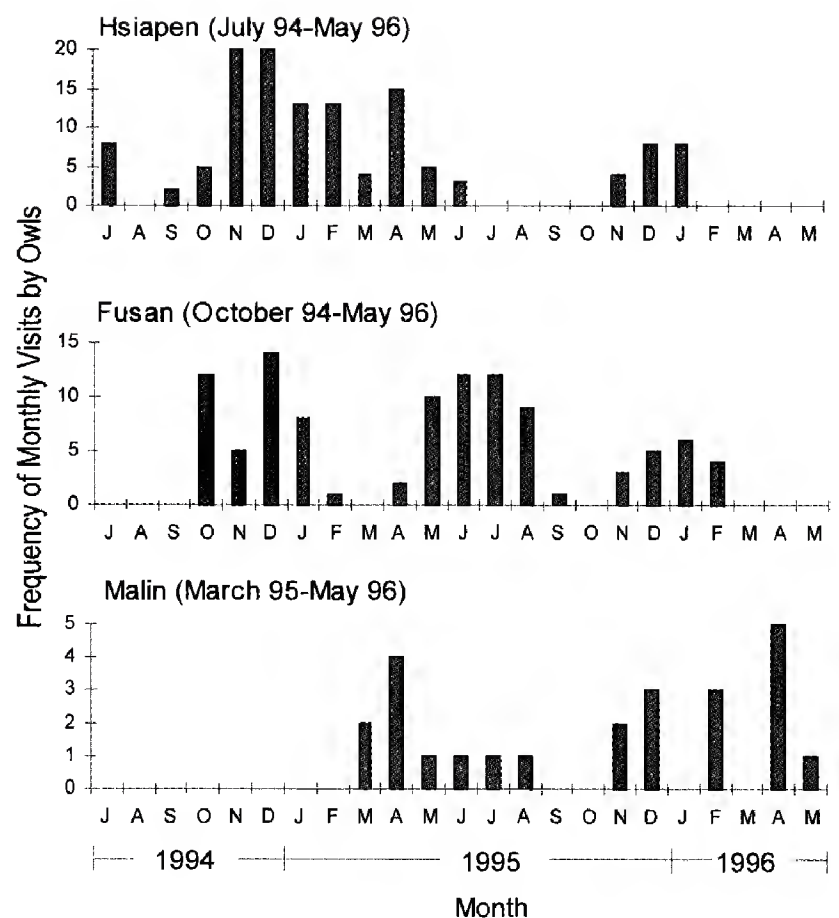


Figure 1. Tawny Fish-Owl foraging trip frequency (number of nights/mo) at cold water fish farms in three owl territories along Nanshih and Tachia streams, Taiwan, 1994–96. Data collected at the Hsiapen and Fusan farms were based on radiotelemetry, and data collected at Malin Farm based on fish remains found on the banks of fish ponds.

highest during the winter. At the Malin Farm, owl predation was highest in April, and it also appeared to increase during November 1995 and February 1996.

We recorded 206 hunting events, including sightings and fish remains, at the five farms. Except for one early morning hunt, hunting only occurred at night. Of the 53 hunts for which the time was known, 28 (52.8%) occurred before midnight. Individual owls visited 1–3 times each night, spending 6–22 min, with a mean of 12.1 min ($SD = 7.0$, $N = 7$ nights), hunting for trout near the water surface. Of 15 foraging attempts observed, five were successful (33.3%). Two trout were eaten immediately on the bank, and the other three were taken into a nearby forest. Sometimes, we found fish scales and remains at foraging perches near the farms. We observed a pair of owls fishing at the Fusan Fish Farm on nine nights. This farm was lit all night by lights. Usually, the owls perched on a nearby snag, immediately adjacent to the fish farm, where they watched for 1–53 min ($\bar{x} = 9.8 \pm 16.4$ min) before flying to the farm.

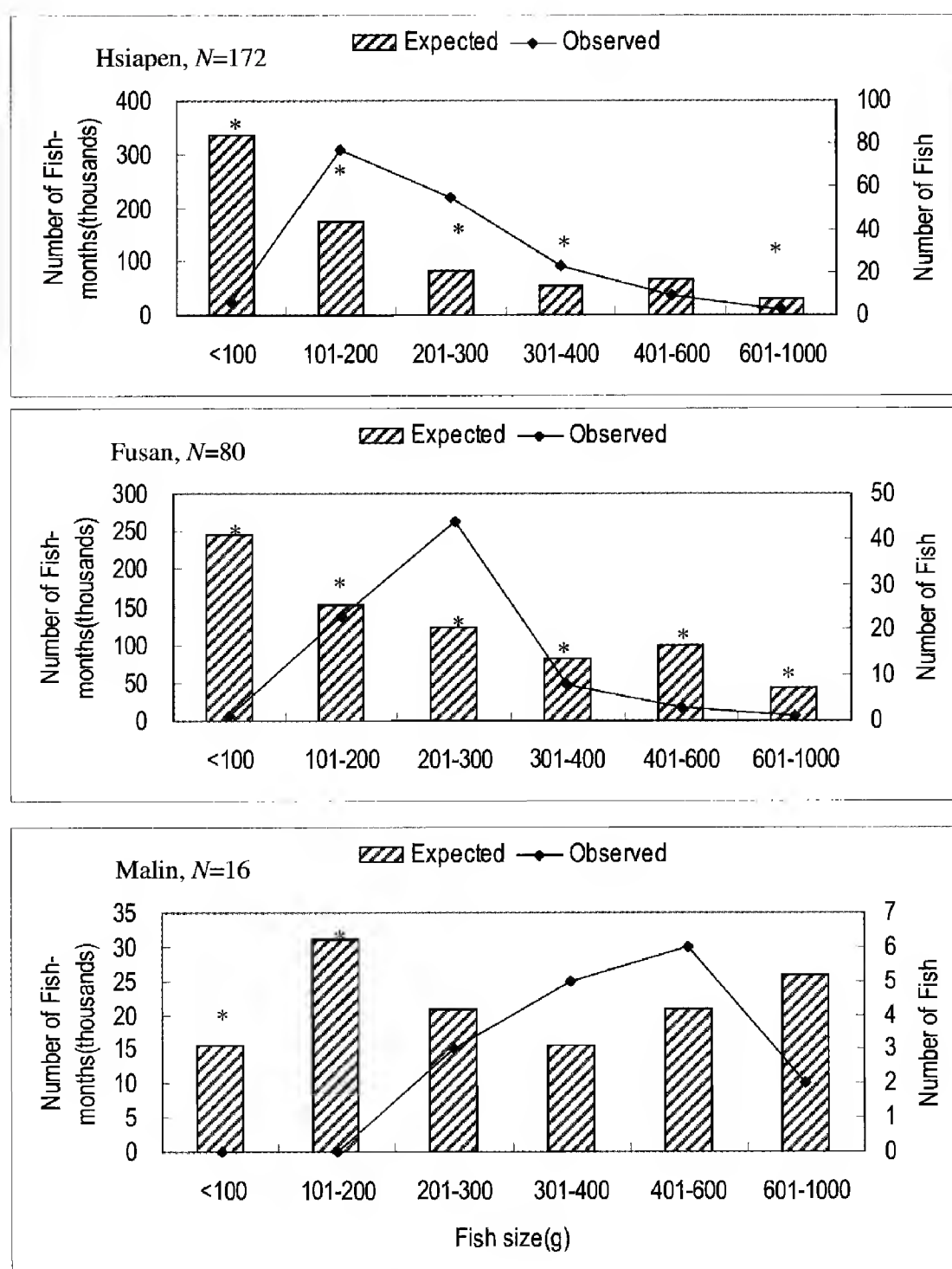


Figure 2. The observed number of fish taken by Tawny Fish-Owls and the availability of fish based estimated fish-months in mass classes (g) at fish farms in Taiwan, July 1994–May 1996. An asterisk (*) indicates $P < 0.05$, Bonferroni Z test.

We found the fresh remains of 60 trout on the banks of fish farms. All trout remains included bloodstains and scales, most also contained gills (77.7%), and some contained the stomach and/or jaws (16.7%). However, only bloodstains and scales were found at fresh ayu remains ($N = 37$). Tawny Fish-Owls took fish ranging from 80–1000 g. They chose fish of specific sizes at Hsiapen ($\chi^2 = 84.2$, $df = 5$, $P = 0.001$), Fusan ($\chi^2 = 46.5$, $df = 5$, $P = 0.001$) and Malin farms (Fisher exact test, $P = 0.004$; Fig. 2). Owls preyed on medium-sized fish (101–400 g) more frequently than expected, and on small fish (<100g) and large fish (>600 g) less often than expected (Bonferroni Z test, $P < 0.05$).

At Malin Farm, owls foraged on slightly larger fish (300–600 g).

In summer, fall, and winter, Tawny Fish-Owls fished on nights with no or light rainfall (Table 1; Bonferroni Z test, $P > 0.05$). In spring, owls foraged slightly more frequently than expected during heavy rain at Fusan and Hsiapen, but this result was not significant ($P > 0.05$; Table 1).

Owls preyed at fish farms more frequently than expected when stream flow was medium and high (Bonferroni Z test, $P < 0.05$). However, the relationship between water flow and owl predation was not significant ($P > 0.05$; Table 2). Small sample size may have been a factor. In all seasons and ar-

Table 1. Tawny Fish-Owl nighttime foraging trips to cold water fish farms in three owl territories in Taiwan, in relation to rainfall and season, July 1994–May 1996.

TERRITORY	SEASON		RAINFALL (mm)		NUMBER OF NIGHTS
			0–10	>10	
Fusan	Summer	Expected	82	10	92
		Observed	21*	0*	21
	Fall	Expected	56	5	61
		Observed	16	1	17
	Spring	Expected	84	8	92
		Observed	13	2	15
Hsiapen	Summer	Expected	54	6	60
		Observed	16*	0*	16
	Fall	Expected	140	12	152
		Observed	45*	1*	46
	Spring	Expected	84	8	92
		Observed	27	5	32
	Winter	Expected	160	18	178
		Observed	53	5	58
	7/95–6/96	Expected	311	23	334
		Observed	33*	0*	33

* Indicates observed value was significantly different than the expected value; $P < 0.05$, Bonferroni Z test.

eas, owls went to fish farms as often, or less often, than expected when water flow was low (Table 2).

From July 1994–June 1996, Tawny Fish-Owls took a total of 288 fish, including 260 trout (90.3%) and 28 ayu (9.7%) from five fish farms in three fish-owl territories (Table 3). At each of the five fish farms, the owls were known to take 8–131 (0.04–0.66%) of ca. 20 000 fish available during the year. The estimated annual cost of the fish taken from each farm ranged from \$18–\$316 US. In 1994–95, owls killed the greatest number of fish at Loshan-chun and Hsinshen farms. In 1995–96, owl predation at these two farms decreased.

DISCUSSION

Tawny Fish-Owls took fish from less than 20% of the cold-water fish farms in Taiwan. We postulate those fish farms at which owls are not a problem do not lie within owl territories because original riparian forests have been eradicated (Sun 1996).

Our data suggested that Tawny Fish-Owls visited fish farms most frequently during the winter. This pattern may have occurred because owls required greater amounts of energy during the cold winter and because fish of suitable sizes were available. For instance, Sun and Wang (1997) reported that the daytime foraging activities of the predominately nocturnal owls were higher in the winter than in other seasons, based on radiotelemetry data.

The stock of fish of the most-often-taken sizes (101–400 g in the Fusan and Hsiapen territories, and 301–600 g at Malin) was greatest in winter, when trout were 8–12 mo old. The availability of these medium-sized classes may have encouraged owl predation. Neither weather, stream flow, nor fish behavior seemed to explain the higher owl predation in the winter. In the study areas, rainfall was lowest during the winter, especially in central Taiwan (Central Weather Bureau 1995). Although rainbow trout that dwelled in deep (>20 m), cold water during the summer, resided in shallower water (<10 m in depth) in winter (Fast 1993), we suggest that seasonal changes in the depth at which fish live do not explain seasonal changes in the incidence of owl predation at fish farms. First, in cold water fish ponds, the water temperature changes very little over the year. Second, the water was less than 1.5 m deep in fish ponds. Finally, sick trout were more common during the hot summer, when water temperatures exceeded 24°C. Sick trout usually swam just beneath the surface, making them easy targets for owls.

Tawny Fish-Owl breeding activity may affect their use of Nanshih Stream fish farms during the spring. In spring 1995, a pair of owls nested in virgin riparian forest along Chakung Stream (Fusan territory), ca. 800 m from two fish farms. From

Table 2. Tawny Fish-Owl hunting trips to cold water fish farms in three owl territories in Taiwan, in relation to water flow and season, July 1994–May 1996.

TERRITORY	SEASON		WATER FLOW			NUMBER OF NIGHTS
			LOW	MEDIUM	HIGH	
Fusan	Summer	Expected	52	37	3	92
		Observed	2	18*	1	21
	Fall	Expected	28	15	18	61
		Observed	0*	5	12*	17
	Winter	Expected	32	43	15	90
		Observed	2*	7	2	11
	Spring	Expected	45	42	5	92
		Observed	8	5	2	15
Hsiapen	Summer	Expected	22	26	16	60
		Observed	4	8	4	16
	Fall	Expected	53	56	43	152
		Observed	1*	41*	4*	46
	Spring	Expected	45	42	5	92
		Observed	12	16	4	32
	Winter	Expected	70	93	15	178
		Observed	13*	35*	10	58
Malin	July 95–June 96	Expected	183	119	32	334
		Observed	18	11	5	34

* Indicates observed value was significantly different than expected value; $P < 0.005$, Bonferroni Z test.

early February to mid-May, the owls stopped visiting the farms. We speculate that the distance between the nest and the farms may have been too great, especially for the male, who delivered food to the female during incubation and to the young during the brood-rearing period (Sun et al. 1997). At Sakatang Stream, pellets, droppings, and prey remains were mostly located within 500 m of the nest of a pair of breeding owls. In addition, for males, nest defense may be more crucial than access to a readily available food source. After mid-May, as more food was needed to feed the young, parent owls may be stimulated to take additional risks and forage at fish farms. In the remaining two

Table 3. Tawny Fish-Owl predation on farmed, cold-water fish and the estimated cost to fish farms in three owl territories in Taiwan, July 1994–96.

DATE	TERRITORY	FISH FARM	NUMBER OF FISH		TOTAL	COST (US)
			TROUT	AYU		
July 94–June 95	Fusan	Hsinshen	55	0	55	208.6
		Fusan	14	0	14	34.9
		Total	69	0	69	243.5
	Hsiapen	Loshanchun	122	9	131	316.3
		Hsiapen	13	8	21	58.3
		Total	135	17	152	364.6
July 95–June 96	Fusan	Hsinshen	21	0	21	79.6
		Fusan	3	5	8	18.0
		Total	24	5	29	97.6
	Hsiapen	Loshanchun	20	2	22	98.5
		Hsiapen	— ^a	—	—	—
		Total	20	2	22	98.5
July 95–June 96	Malin	Malin	16	0	16	60.4

^a Data not recorded.

territories and other areas surveyed, variation in the predation rates during the spring and summer may have resulted from the distance between nesting sites and fish farms. In Taiwan, most fish farms were built near developed riparian zones in lowland areas. Tawny Fish-Owls are unlikely to nest near these farms or forage at them during the breeding season.

Mist netting was not as effective as steel leg-hold traps in capturing Tawny Fish-Owls that preyed on farm fish. This was because mist nets were erected to capture smaller predatory birds such as the Black-crowned Night Heron (*Nycticorax nycticorax*), a common nuisance in Taiwan. Therefore, the owls often can escape after initial entanglement. Tawny Fish-Owls can become trapped in pond water and drown. Poole (1989) proposed that drowned Ospreys were not pulled into the water by the large fish they seized. He argued that Ospreys, with the ability to catch prey weighing up to 1500 g, could readily remove their talons from prey if they were too heavy. No fish were found in the talons of injured or drowned Tawny Fish-Owls. However, the Tawny Fish-Owls we found in ponds containing large trout (>600 g). Photographs taken with an automatic camera placed at a fish pond revealed that fish-owls catch fish by plunging into the water, as do Osprey (Poole 1989). Blakiston's Fish-Owls (*K. blakistoni*) were also seen catching fish by plunging into the water (Yamamoto 1988). We assume that catching large fish takes more energy and increases the chance of a struggle in the water. Thus, the chance of injury and death may increase with fish mass, especially for slow-flying birds, such as most owls (Norberg 1987). Two owls preying on small fish also were trapped in the water. In these cases, we believe the strong current in the circular pond, which has an outlet in the center that generates a vortex, was probably responsible for these accidents. We also suggest that owls that fish near the outlet could be sucked into the vortex.

During this study, the fishing success of Tawny Fish-Owls at fish farms was 33.3%, somewhat lower than that of the Blakiston's Fish-Owl (45–50%) in a stream (Yamamoto 1988). Usually, Tawny Fish-Owls spent <1 hr fishing at a fish farm. The owls could quickly catch all the fish they needed because prey was abundant and they eat only 114–228 g of prey per day (Sun 1996).

Owls tended to avoid foraging at fish farms when it rained hard at night. Heavy rain also might reduce or stop owl foraging in streams by making it

difficult for owls to detect prey. After moderate rains made the water in Nanshih Stream turbid, Tawny Fish-Owl hunting of farmed trout increased. This likely occurred because fish-pond water remained clear. Most of the small creeks that provide water for the fish ponds drain heavily-vegetated slopes. Water in these smaller streams remained clear during and after moderate rain. Consequently, owls foraged at the fish farms when ponds were clear. However, heavy rains made the water of small creeks and fish ponds turbid, probably decreasing owl predation.

Most farm fish caught by Tawny Fish-Owls weighed 101–400 g, or 4.1–16.5% of the owls' body mass (2200–2650 g). The prey/predator body mass ratio for Osprey, which catches 150–300 g fish, was also 8.3–16.7% (Poole 1989). We saw a number of large farm trout (600–1000 g) with scratches on both flanks, suggesting an owl had tried and failed to capture the fish.

After owls were captured and released at fish farms, they seemed to reduce their hunting at these facilities. In 1994–95, owls killed fewer fish at the Fusan and Hsiapen farms, compared to the Hsinshen and Loshanchun farms. This probably occurred because we first trapped, marked, and released two owls each at the Fusan and Hsiapen farms in the fall of 1993. In 1995–96, we captured, marked, and released the two owls that used the Hsinshen Farm within the Fusan territory, and one owl that used the Loshanchun Farm, of the Hsiapen territory, again causing a decrease in predation at the farms again. Specifically, the number of fish eaten by owls decreased by 83.2% and 61.8% at the Hsinshen and Loshanchun farms, respectively.

Lower owl depredation at Malin probably resulted from other factors, such as an increase in natural prey abundance and effective use of dogs as an aversion measure. The Fusan Farm owner even used the presence of Tawny Fish-Owls to attract birders and photographers, who paid boarding fees. Based on our data, fish farmers were relieved to find out losses to owls were relatively minimal.

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GEOGRAPHIC VARIATION IN MORPHOLOGY OF FOUR SPECIES OF MIGRATORY RAPTORS

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ABSTRACT.—We studied geographic variation in morphology of four species of migratory raptor to test large-scale hypotheses of adaptive divergence in quantitative characters among migratory flyways. The Sharp-shinned Hawk (*Accipiter striatus*), Cooper's Hawk (*Accipiter cooperii*), Red-tailed Hawk (*Buteo jamaicensis*), and American Kestrel (*Falco sparverius*) are co-distributed throughout North America. We examined patterns of morphological variation among raptors migrating along two western flyways, the Goshute Mountains of Nevada and Manzano Mountains of New Mexico, and one eastern flyway, Cape May Point in New Jersey. Although they were lower in mass, raptors from western flyways had significantly longer wings, longer tails or both, compared to conspecifics from an eastern flyway. It is significant that parallel variation in flight morphology occurs across four taxa that differ widely in taxonomic affinity, flight habits, size, and shape.

KEY WORDS: *Sharp-shinned Hawk*; *Accipiter striatus*; *Cooper's Hawk*; *Accipiter cooperii*; *Red-tailed Hawk*; *Buteo jamaicensis*; *American Kestrel*; *Falco sparverius*; *ecomorphology*; *migration*; *principal components analysis*.

VARIACIÓN GEOGRÁFICA EN LA MORFOLOGÍA DE CUATRO ESPECIES DE RAPACES MIGRATORIAS

RESUMEN.—Estudiamos la variación geográfica en la morfología de cuatro especies de rapaces migratorias para evaluar hipótesis a gran escala sobre la divergencia adaptativa en caracteres cuantitativos entre rutas migratorias. *Accipiter striatus*, *Accipiter cooperii*, *Buteo jamaicensis*, y *Falco sparverius* se encuentran co-distribuidos en América del Norte. Examinamos los patrones de variación morfológica entre las rapaces encontradas migrando a lo largo de dos rutas migratorias del oeste, las montañas Goshute de Nevada y las montañas Manzano de New Mexico, y una ruta del este, Cape May Point en New Jersey. Aunque presentaron menor masa corporal, las rapaces de las rutas del oeste tuvieron alas significativamente más largas, colas significativamente más largas, o ambas, comparadas con aves coespecíficas de la ruta del este. Es significativo que exista variación paralela en la morfología del vuelo en cuatro taxa que difieren enormemente en afinidad taxonómica, hábitos de vuelo, tamaño y forma.

[Traducción del equipo editorial]

Species with wide distributions are often exposed to a variety of environmental conditions that may result in a number of populations having unique morphologies that reflect local conditions. Evolutionary responses to natural selection associated with environmental variation may consist of population-level genetic divergence or phenotypic plasticity (James 1983, 1991, Via and Lande 1985,

Bull 1987). Studies of geographic variation in avian populations have documented differences in body size, wing length, leg and foot shape, and bill size and shape that have been correlated with variation in climate, habitat, or ecology (e.g., James 1970, 1991, Wattel 1973, Leisler et al. 1989, Whaley and White 1994, Fitzpatrick and Dunk 1999).

In this study, we examine geographic variation of morphology within four species of migratory raptors to determine the degree to which different species exhibit concordant patterns. If there is geographic variation in morphology, it might be attributed to environmental conditions in breeding or wintering habitat. James (1991) found that birds

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from cool, dry climates tend to be large while those from warm, humid climates tend to be small as predicted by Bergmann's rule. Alternatively, migration patterns and habits may influence morphology and be exhibited in wing and tail characteristics relative to body size.

Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*A. cooperii*), Red-tailed Hawks (*Buteo jamaicensis*), and American Kestrels (*Falco sparverius*) are all found throughout North America with many populations exhibiting seasonal north-south migration. Individuals were sampled from two migratory routes in western North America and one on the east coast. While little can be said about the breeding grounds for birds captured on migration, some hypotheses can be developed regarding migratory patterns and some general statements about potential adaptations to wintering and breeding habitat can be made.

The Goshute Mountains of Nevada and the Manzano Mountains of New Mexico are monitoring points along major raptor flyways in the west (Hoffman et al. 2002), and Cape May Point in New Jersey is situated on a major eastern flyway (Clark 1985). The Goshute and Manzano mountain flyways are both situated along mountainous-ridge systems. Migrants through Cape May Point build up along the Atlantic coastline and funnel into the southern New Jersey peninsula to cross the Delaware Bay. Based on available band returns, breeding grounds are thought to be north of the western flyways (Smith et al. 1990, Hoffman et al. 2002), and north and east of the eastern flyway (Clark 1985, W. Clark pers. comm.). Goshute and Manzano migrants travel each fall to wintering grounds in central and western Mexico, a distance that may be as much as twice that of eastern migrants, which tend to remain in the southeastern United States (Clark 1985, Smith et al. 1990, W. Clark pers. comm.). The wintering grounds of raptors provide important habitat for a substantial portion of the year.

Consistent variation in morphology across taxa is supportive of the idea that ecological or environmental factors may drive such patterns. The single flight-related activity that all these species have in common (western vs. eastern populations) is their migratory pattern. With flights through the Manzanos and Goshutes occurring in high-altitude-arid mountains and continuing for longer distances, greater flight surfaces may decrease wing loading, and hence may increase flight efficiency in these

habitats. A habitat-related variable on both breeding and wintering grounds that might influence body size would be climate. However, we were unable to make specific predictions with regards climate and body size without additional information as to the origin and destination of the birds.

METHODS

Morphological Variables. Between September and November 1991–94 we collected mensural information from raptors trapped while in migration on each of three flyways. We measured mass, length of central rectrix (Tail), wing chord (Wing), tarsus length (Tarsus Length), tarsus width at the narrowest point (Tarsus Width), culmen length (Culmen; bill from cere to tip) and hallux length (Hallux; length of hind claw) using a balance, dial calipers, metric ruler, and wing-chord ruler. In the absence of wing and tail surface area measurements, wing and tail length were taken to be indicators of flight-surface area. Flight-surface area is a function of length and width, and wing area increases proportionally as a square of wing span in wings of similar shape (Tucker and Parrott 1970, Pennycuik 1975). Any birds with a noticeable crop were removed from analyses involving body mass. Sharp-shinned Hawks, Cooper's Hawks, and American Kestrels were grouped according to gender and age because of sexual dimorphism and differential growth of feathers. Red-tailed Hawks were grouped only by age. Results are reported for hatch-year birds only; samples of adult birds were too small for statistical analyses.

We log-transformed all measurements to conform to a multivariate-normal distribution and compared character by character using StatGraphics (Manguistics, Inc., Rockville, MD U.S.A.) multiple analysis of variance. We also performed multivariate analyses to remove possible allometric relationships and to investigate morphological shape variables. Principal component scores were determined for each species and gender, after which scores were assigned to individuals. For the principal components analysis, mass was eliminated from analyses of size and shape because it was highly variable and may have simply reflected the physical condition of migrants. We used analysis of variance to test for significant differences between flyways for each component score. Correlation analysis of the first three principal components and the morphological measurements was also performed.

RESULTS

Univariate Analyses. With the exception of marginal pattern in the female Sharp-shinned Hawk, all four species of raptor and both genders were significantly heavier in the east than in the west (Tables 1–4). Sharp-shinned Hawks averaged 5% heavier in the east than in the west, American Kestrels were 7% (males) and 9% (females) heavier in Cape May than in the west, Red-tailed Hawks were about 17% heavier in the east than in the west, and Cooper's Hawks showed the greatest difference at 23% (males) and 29% (females) heavier in the east

Table 1. Results of multiple analysis of variance for significant differences in mean morphological characters of male and female hatch-year Sharp-shinned Hawks in three flyways. Significant differences are represented by unique letters for flyways. Standard deviations are in parentheses. Mass was given in grams and linear measurements in millimeters. Values for males are in the first line, females in the second.

CHARACTER	GOSHUTES	MANZANOS	CAPE MAY	P-VALUE
MALES	N = 100	N = 21	N = 24	
FEMALES	N = 87	N = 9	N = 37	
Mass	98.3 (6.3) ^a	98.4 (7.1) ^a	102.9 (7.1) ^b	0.009
	162.9 (12.2) ^a	170.1 (15.5) ^{ab}	170.5 (15.6) ^b	0.016
Tail	138.4 (3.0) ^a	139.3 (3.5) ^a	131.5 (4.9) ^b	<0.001
	162.7 (5.0) ^a	160.0 (6.3) ^a	154.1 (5.4) ^b	<0.001
Wing	170.7 (2.9) ^a	172.3 (2.7) ^b	164.8 (4.2) ^c	<0.001
	202.2 (4.1) ^a	202.4 (4.5) ^a	195.6 (4.7) ^b	<0.001
Tarsus length	50.4 (1.2) ^a	49.6 (1.0) ^b	48.7 (1.8) ^c	<0.001
	56.3 (1.4) ^a	54.8 (1.9) ^b	55.2 (1.6) ^b	<0.001
Tarsus width	3.4 (0.2) ^a	3.6 (0.1) ^b	3.5 (0.2) ^b	0.001
	4.3 (0.3) ^a	4.4 (0.3) ^{ab}	4.5 (0.3) ^b	0.003
Hallux	11.4 (0.4) ^a	11.4 (0.4) ^a	11.1 (0.5) ^b	0.001
	14.3 (0.5) ^a	14.3 (0.6) ^a	14.3 (0.6) ^a	0.944
Culmen	9.8 (0.3) ^a	9.7 (0.4) ^a	10.0 (0.4) ^b	0.006
	11.9 (0.4) ^a	11.9 (0.3) ^a	12.2 (0.5) ^b	<0.001

than in the west. Three species had significantly longer mean wing and tail length in the west than in the east, with the exception of the Cooper's Hawk.

Leg length and width also varied between flyways. There was a tendency for raptors migrating

through the Goshute Mountains to have longer and/or thinner tarsi than other migrants but the pattern was not significant for all species. Culmen length was longest in Cape May for Sharp-shinned Hawks, female Cooper's Hawks and Red-tailed Hawks.

Table 2. Results of analysis of variance for significant difference in morphological characters between flyways for male and female hatch-year Cooper's Hawks. Significant differences are represented by unique letters for flyways. Standard deviations are in parentheses. Mass was measured in grams and linear measurements in millimeters. Values for males are in the first line, females in the second.

CHARACTER	GOSHUTES	MANZANOS	CAPE MAY	P-VALUE
MALES	N = 37	N = 36	N = 37	
FEMALES	N = 28	N = 39	N = 21	
Mass	253.7 (15.5) ^a	266.6 (26.0) ^a	339.2 (38.7) ^b	<0.001
	378.5 (25.9) ^a	400.5 (35.5) ^b	530.3 (41.0) ^c	<0.001
Tail	188.8 (6.4) ^a	194.3 (5.1) ^b	191.0 (5.6) ^a	<0.001
	214.1 (8.1) ^a	217.2 (6.6) ^a	216.9 (7.8) ^a	0.254
Wing	220.1 (4.8) ^a	226.0 (5.0) ^b	228.0 (4.9) ^c	<0.001
	251.5 (4.8) ^a	255.2 (5.9) ^b	260.1 (6.7) ^c	<0.001
Tarsus length	62.2 (1.9) ^a	61.7 (1.6) ^a	65.0 (1.8) ^b	<0.001
	68.6 (2.1) ^a	67.3 (2.3) ^b	73.2 (1.8) ^c	<0.001
Tarsus width	5.4 (0.3) ^a	5.7 (0.3) ^b	6.0 (0.5) ^c	<0.001
	6.6 (0.4) ^a	7.1 (0.4) ^b	7.4 (0.5) ^c	<0.001
Hallux	18.8 (0.6) ^a	18.8 (0.6) ^a	19.7 (0.6) ^b	<0.001
	22.3 (0.8) ^a	22.2 (0.6) ^a	23.8 (1.7) ^b	<0.001
Culmen	14.7 (0.5) ^a	14.7 (1.1) ^a	14.9 (2.0) ^a	0.715
	17.2 (1.2) ^a	17.0 (1.5) ^a	19.2 (0.9) ^b	<0.001

Table 3. Results of analysis of variance for significant differences in morphological characters between flyways for hatch-year Red-tailed Hawks. Significant differences are represented by unique letters for flyways. Standard deviations are in parentheses. Mass was measured in grams and linear measurements in millimeters.

CHARACTER	GOSHUTES N = 152	MANZANOS N = 62	CAPE MAY N = 12	P-VALUE
Mass	933.4 (150.5) ^a	950.2 (124.3) ^a	1134.4 (143.6) ^b	<0.001
Tail	233.7 (11.3) ^a	235.8 (11.0) ^a	222.1 (9.5) ^b	<0.001
Wing	397.4 (17.2) ^a	403.6 (17.2) ^b	387.3 (14.8) ^a	0.004
Tarsus length	87.7 (4.2) ^a	88.5 (4.2) ^a	85.8 (9.0) ^a	0.145
Tarsus width	10.8 (0.9) ^a	11.0 (0.8) ^a	12.8 (0.7) ^b	<0.001
Hallux	28.8 (2.0) ^a	29.2 (1.6) ^a	32.6 (2.2) ^b	<0.001
Culmen	25.1 (1.4) ^a	25.1 (1.4) ^a	28.1 (1.4) ^b	<0.001

Multivariate Analyses. The first principal component (PC1) was interpreted as an overall size component in the Cooper’s Hawk and Red-tailed Hawk (Fig. 1). This component explained 37% and 45% of the variation in male and female Cooper’s Hawks, respectively, and 59% of the variation in Red-tailed Hawks. Weightings (Manly 1994) of all the characters were, generally, equally high. Val-

ues of PC1 were highest for wing and tail, with values for other characters being lower, in the Sharp-shinned Hawk and in the American Kestrel (Fig. 1). This component explained 32% and 33% of the variation in male and female Sharp-shinned Hawks, and 27% and 29% of the variation in male and female American Kestrels.

Individuals of all four species were significantly

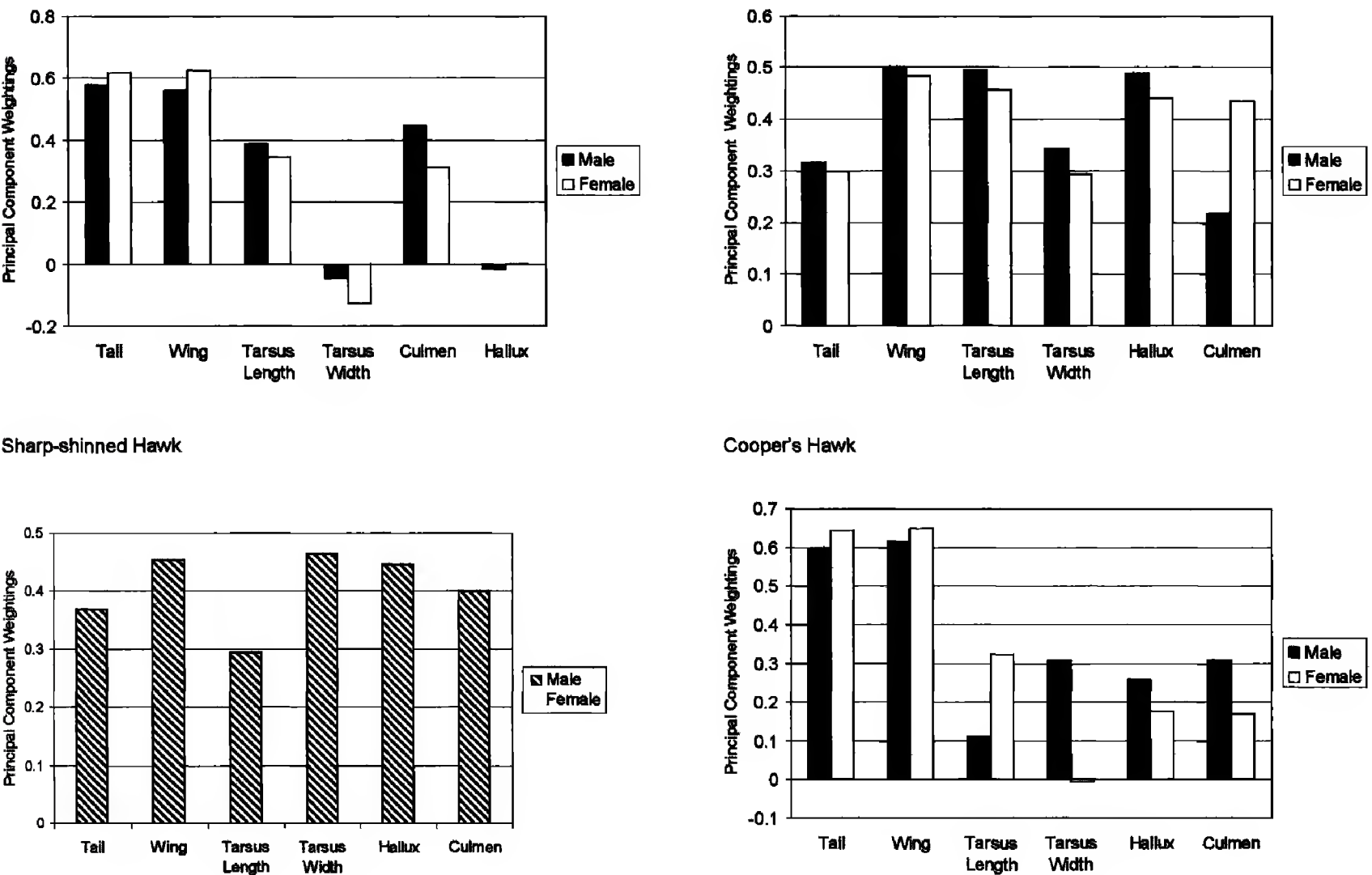


Figure 1. Principal component weightings (PC1) for six morphological variables (Tail = tail length, Wing = wing length, tarsus length, tarsus width, Hallux = hallux length, and Culmen = culmen length) are presented as bar graphs. Genders could not be distinguished in Red-tailed Hawks.

Table 4. Results of analysis of variance for significant differences in morphological characters between flyways for male and female hatch-year American Kestrels. Significant differences are represented by unique letters for flyways. Standard deviations are in parentheses. Mass was measured in grams, linear measurements are in millimeters. Values for males are in the first line, females in the second.

CHARACTER	GOSHUTES	MANZANOS	CAPE MAY	P-VALUE
MALES	N = 205	N = 21	N = 14	
FEMALES	N = 158	N = 13	N = 13	
Mass	100.9 (7.9) ^a	102.5 (7.6) ^a	109.6 (10.2) ^b	0.001
	107.6 (9.1) ^a	114.1 (9.7) ^b	121.7 (7.5) ^c	<0.001
Tail	121.9 (4.9) ^a	121.1 (6.2) ^a	116.4 (4.5) ^b	0.0001
	126.6 (5.3) ^a	124.5 (7.3) ^{ab}	121.8 (3.3) ^b	0.005
Wing	188.7 (5.6) ^a	191.6 (5.3) ^b	180.1 (5.5) ^c	<0.001
	197.1 (6.1) ^a	196.7 (8.5) ^a	191.2 (5.7) ^b	0.005
Tarsus length	36.4 (2.1) ^a	35.6 (1.6) ^b	35.5 (2.5) ^{ab}	0.050
	36.3 (1.9) ^a	35.6 (2.0) ^a	35.4 (1.7) ^a	0.152
Tarsus width	4.1 (0.3) ^a	4.1 (0.4) ^a	3.8 (0.2) ^b	0.011
	4.2 (0.4) ^a	4.4 (0.4) ^b	4.3 (0.4) ^{ab}	0.083
Hallux	9.4 (0.5) ^a	9.8 (0.7) ^a	9.5 (0.5) ^a	0.704
	9.8 (0.7) ^a	9.7 (0.5) ^a	9.8 (0.4) ^a	0.954
Culmen	11.6 (0.6) ^a	11.6 (0.7) ^a	11.8 (0.8) ^a	0.254
	11.9 (0.7) ^a	12.3 (0.6) ^a	12.2 (0.5) ^a	0.083

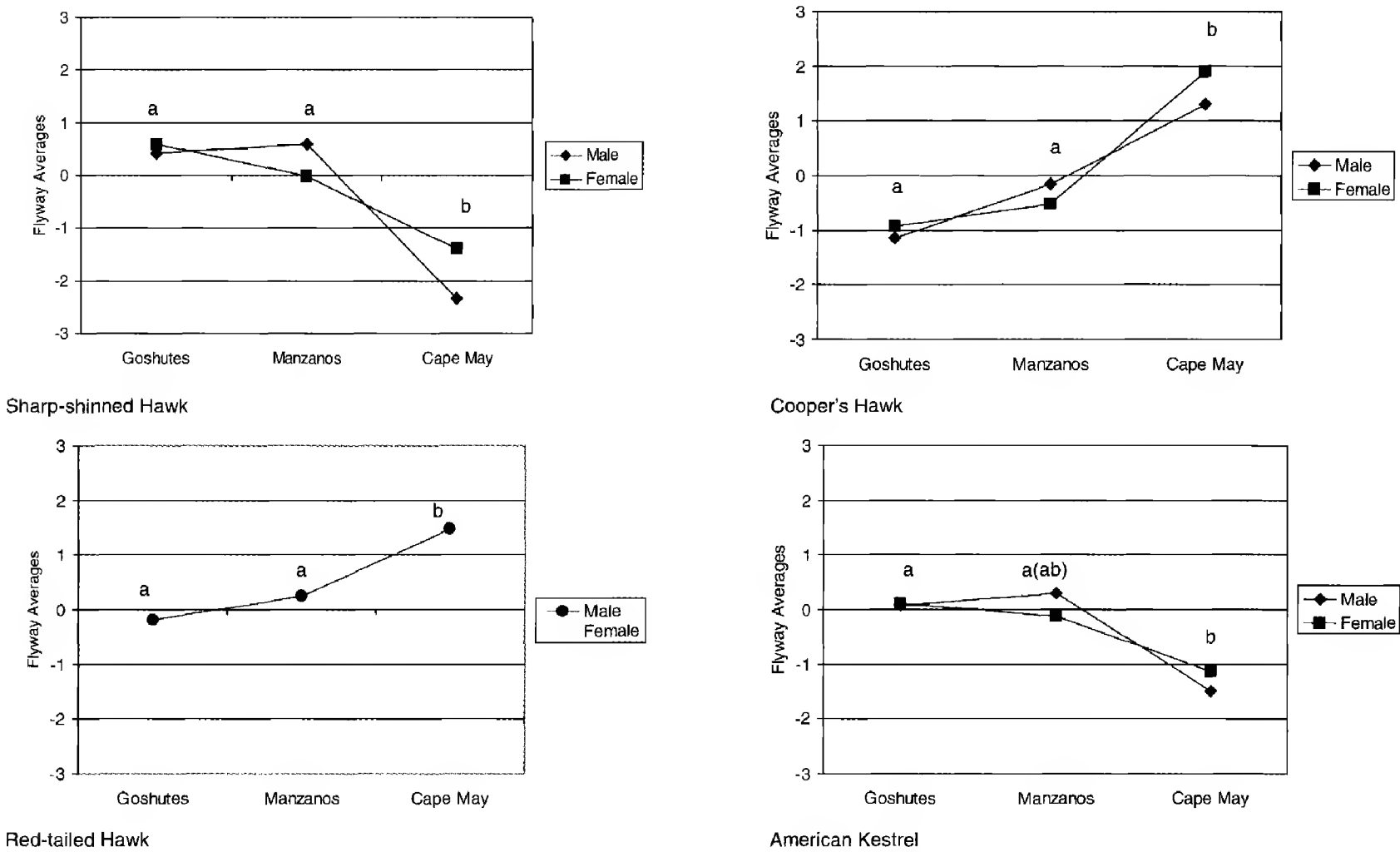


Figure 2. Principal component 1 scores (y-axis) were assigned to individuals and significant differences between flyways were determined by analysis of variance. Significantly different means ($P < 0.05$) for flyways (Goshute Mountains, Manzano Mountains, and Cape May Point) are indicated by unique letters. Genders could not be distinguished in Red-tailed Hawks.

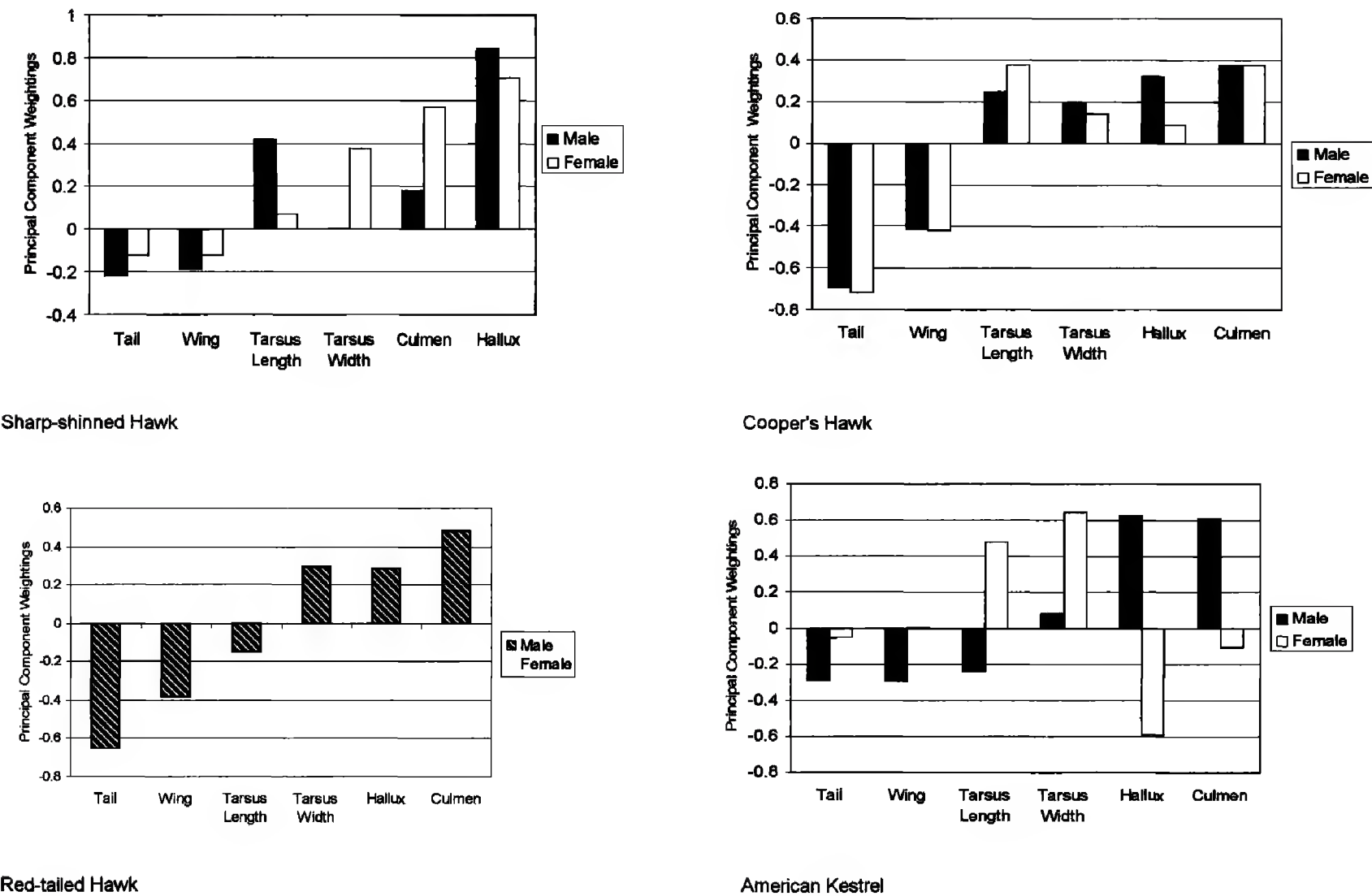


Figure 3. Principal component weightings (PC2) for six morphological variables (Tail = tail length, Wing = wing length, tarsus length, tarsus width, Hallux = hallux length, and Culmen = culmen length) are presented as bar graphs. Genders could not be distinguished in Red-tailed Hawks.

different for mean PC1 scores between eastern and western flyways except for female American Kestrels, which were significantly different only between Goshute Mountains and Cape May Point (Fig. 2). The general pattern indicated large overall size in eastern Cooper's Hawk and Red-tailed Hawk migrants, and long mean wings and tail in western Sharp-shinned Hawks and American Kestrels.

PC2 was interpreted to be a shape component in Cooper's and Red-tailed hawks (Fig. 3). Tail and wing loaded opposite to other characters. Cooper's Hawks migrating through the Manzano Mountains were significantly different for mean PC2 scores from those migrating through the other flyways and had longer tails than Goshute and Cape May migrants (Table 2, Fig. 4). This component explained 19% and 20% of the variation in male and female Cooper's Hawks, and 13% of the variation in Red-tailed Hawks. Red-tailed Hawks migrating through Cape May Point were significantly different from the other flyways for this component and

had shorter wings and tail than western migrants (Table 3, Fig. 3). On the other hand, PC2 consisted of variable weightings of culmen, hallux, and leg characters in Sharp-shinned Hawks and American Kestrels (Fig. 3). PC2 explained 19% and 20% of the variation in male and female Sharp-shinned Hawks, and 18% of the variation in both sexes of the American Kestrel. Although there were significant differences between some flyways (Fig. 4), variation for this component was difficult to interpret in the smaller raptors.

DISCUSSION

Four species exhibited considerable variation in size, taxonomy, predatory habits, and flight styles, yet we found a common pattern of morphological variation. The four species of raptors exhibited geographic variation in morphology among migratory flyway pathways. We were unable to correlate variation in body size with climate due to uncertainty of specific geographic location of either breeding or migratory habitat. The morphological

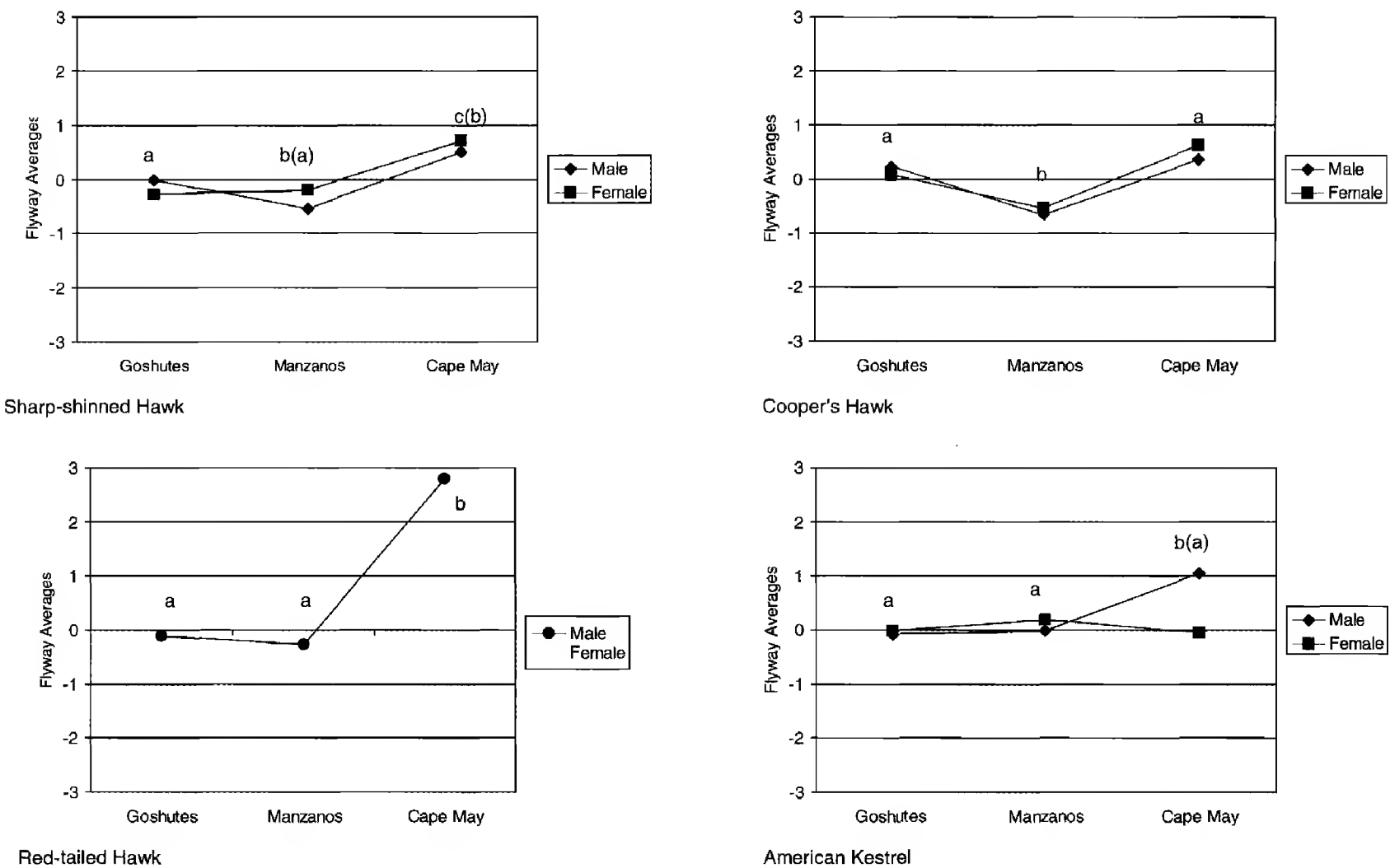


Figure 4. Principal component 2 scores (y-axis) were assigned to individuals and significant differences between flyways were determined by analysis of variance. Significantly different means ($P < 0.05$) for flyways (Goshute Mountains, Manzano Mountains, and Cape May Point) are indicated by unique letters. Genders could not be distinguished in Red-tailed Hawks.

patterns observed could result from either genetic differentiation for the traits or from phenotypic plasticity (James 1983). Of the four species in this study, only the Red-tailed Hawk consists of a number of subspecies or races in North America in the area of the study (Preston and Beane 1993). In a separate study using mitochondrial DNA (mtDNA) from the same individuals, only the Red-tailed Hawk exhibited genetic differences between eastern and western flyways indicating population genetic structure (Pearlstone 2004).

Morphological Variation and Migration Distance. The Sharp-shinned Hawk, Red-tailed Hawk, and American Kestrel exhibited variation in body mass, wing chord, and tail length consistently among the migratory flyways, whereas the Cooper's Hawk did not. Although wing area was not measured, we used wing length as an approximate indication of relative wing area within a species. Increased wing length in western raptors may result in greater wing area, thus reducing wing loading, and perhaps the cost of migratory flight. In contrast to the

raptors in this study, migratory populations of passerines do not have longer wings but they are more pointed than nonmigratory populations (Mulvihill and Chandler 1991, Senar et al. 1994, Monkkonen 1995). There is a difference in flight strategy, however, as small birds migrate primarily through flapping flight, whereas raptors tend to utilize gliding and soaring strategies to minimize flight costs (Kerlinger 1989, Alerstam 1990).

The tail is also a vital component of flight surface in birds, especially when lift is important (Thomas and Balmford 1995). Raptors can reduce wing loading by from 19.7% (Red-tailed Hawks) to 29.3% (Sharp-shinned Hawks) by simply spreading the tail (Kerlinger 1989). Despite the smaller body mass of western migrants, wings and tail were significantly longer in Sharp-shinned and Red-tailed hawks relative to Cape May migrants. Wings and tail were significantly longer in male American Kestrels from the west than from the east and wings were significantly longer in western female American Kestrels than eastern. Parallel variation be-

tween the three species from three flyways suggests possible natural selection relative to migration.

Morphological Variation and Climate. Variation in body mass among the three flyways revealed consistently larger body size in the east than in the west. Mean mass for all species was greater in the east, and PC1 in the large raptors supports the observation of relatively large eastern individuals for Cooper's and Red-tailed hawks. Other studies of geographic variation correlated with climate have provided support for Bergmann's rule, though not for the same geographic areas as this study (James 1970, Aldrich 1984, Murphy 1985, Aldrich and James 1991). A comprehensive review of avian morphology by Zink and Remsen (1986) however, revealed that only 42% of studies provide unambiguous evidence of correlation between body size and climate. One study of Red-tailed Hawks also failed to support variation in body size according to Bergmann's rule (Fitzpatrick and Dunk 1999). Additionally, predictions from Bergmann's rule have not been supported for migratory species. The variation in body size revealed by this study was consistent with results of Zink and Remsen's (1986) analysis. Bergmann's rule may hold true however, for body size comparisons made with respect to wintering habitat (e.g., Johnston and Fleischer 1981, Wiedenfeld 1991). Clearly, raptors must be studied on both wintering and breeding grounds to further understand this pattern.

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HOME-RANGE SIZE OF THE JAVAN HAWK-EAGLE (*SPIZAETUS BARTELSI*) ESTIMATED FROM DIRECT OBSERVATIONS AND RADIOTELEMETRY

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ABSTRACT.—The mean home-range size of the Javan Hawk-Eagle (*Spizaetus bartelsi*) on Java was estimated to be ca. 400 ha based on three different methods. The distance between nests of neighboring pairs was ca. 3 km in Gede-Pangrango and 2 km in the Salak Mountains. In the Halimun Mountains, the mean distance between territories was 1.8 km. Radiotracking of one adult male indicated a home-range size of 300 ha in the nonbreeding season. This finding suggested that earlier population estimates probably were too low, as they were based on home-range estimates of 2000–5000 ha per pair depending on habitat quality. The species should still be considered endangered, as it is threatened both from habitat loss and illegal hunting.

KEY WORDS: *Javan Hawk-Eagle*, *Spizaetus bartelsi*; *home range*, *population status*, *radio-tracking*, *Indonesia*.

TAMAÑO DEL ÁREA DE HOGAR DE *SPIZAETUS BARTELSI* ESTIMADO A PARTIR DE OBSERVACIONES DIRECTAS Y RADIOTELEMETRÍA

RESUMEN.—El tamaño medio del área de hogar de *Spizaetus bartelsi* en Java ha sido estimado en aproximadamente 400 ha considerando tres métodos distintos. La distancia entre los límites de las áreas de hogar de parejas vecinas fue de aproximadamente 3 km en Gede-Pangrango y 2 km en las montañas de Salak. En las montañas de Halimun, la distancia media entre territorios fue de 1.8 km. El seguimiento con radiotransmisores de un macho adulto indicó un área de hogar de 300 ha en la estación no reproductiva. Esto sugirió que las estimaciones poblacionales anteriores fueron probablemente muy bajas, ya que estuvieron basadas en estimaciones de áreas de hogar de 2000–5000 ha por pareja, dependiendo en la calidad del hábitat. La especie debe aún ser considerada en peligro, ya que está amenazada tanto por la pérdida de hábitat como por la cacería ilegal.

[Traducción del equipo editorial]

The Javan Hawk-Eagle (*Spizaetus bartelsi*) is endemic to the rainforests of Java, Indonesia, where less than 10% of the original natural forests remain (Whitten et al. 1996). Small population size, severe habitat loss, forest fragmentation, and illegal hunting have all contributed to the “endangered” status of this species on the world list of threatened

birds (BirdLife International 2000, BirdLife International 2001). The population size has been estimated differently by various authors; “Not more than 60 breeding pairs” (Meyburg et al. 1989), “67–81 pairs” (van Balen and Meyburg 1994), “81–108 pairs” (Sözer and Nijman 1995), and “137–188 pairs” (van Balen 1999, van Balen et al 2000). These estimates were based on data on the size of two home ranges. Thiollay and Meyburg (1988) estimated the home-range size to be 2000–

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3000 ha, but used 1700–4500 ha when they calculated their population estimates. Meyburg et al. (1989) suggested that suboptimal habitat may support home ranges as large as 12 000 ha. The home-range size of a breeding male studied in west Java was estimated at a minimum of 1200 ha (Sözer and Nijman 1995), and of another adult in central Java at ca. 3600 ha (van Balen 1999).

To obtain accurate knowledge of population size, it is necessary to obtain reliable data on density and area of suitable habitat. Density estimates have usually been based on the size of a few home ranges mapped by sight observations (Meyburg et al. 1989, Sözer and Nijman 1995, van Balen and Meyburg 1994, van Balen et al. 2000) under the assumptions that the eagle pairs occupy contiguous breeding territories and that entire forest areas are used by breeding pairs. We studied the home range of the Javan Hawk-Eagle in western Java by three different methods: (1) direct observation of territorial behavior of breeding pairs, (2) the distances between nests, and (3) radio-tracking of one adult male.

Distance between neighbor pairs was defined as the distance between the centroids of their territories. When nests were known, we used the distance between occupied nests of the same year. In this paper, we assume that home range is the same as territory, as the entire home range seems to be defended by Javan Hawk-Eagles during the breeding season (pers. obs.).

STUDY AREA AND METHODS

Halimun. This study area is close to Ciptarasa village on the slopes of the Halimun Mountains in west Java, and is close to and partly inside Halimun National Park (Fig. 1). Most observations were made from open cultivated areas along the forest borders. The rainforests were of lowland or lower-montane type at ca. 1000 m above sea level (masl). The national park is comprised of ca. 20% lowland forest (Whitten et al. 1996). Halimun National Park (established 1992) covers an area of 40 000 ha (Whitten et al. 1996) and is one of the largest forested areas in Java. Around it are large forested areas in administrative management as production or protected forests. Relatively large areas of primary rainforest still exist outside the borders of the park. However, because of need for cultivated land, the surrounding forests are gradually transformed into gardens and rice fields. Annual rainfall is between 4000–6000 mm. During large parts of the year, the highest mountains are covered by mist and fog, which its Indonesian name indicates.

Mt. Salak. This mountain is a volcano 2211 masl, well vegetated to the top (Fig. 1). The area of forest containing Javan Hawk-Eagle has been estimated to 10 000 ha (van Balen et al. 1999). The forests have administrative

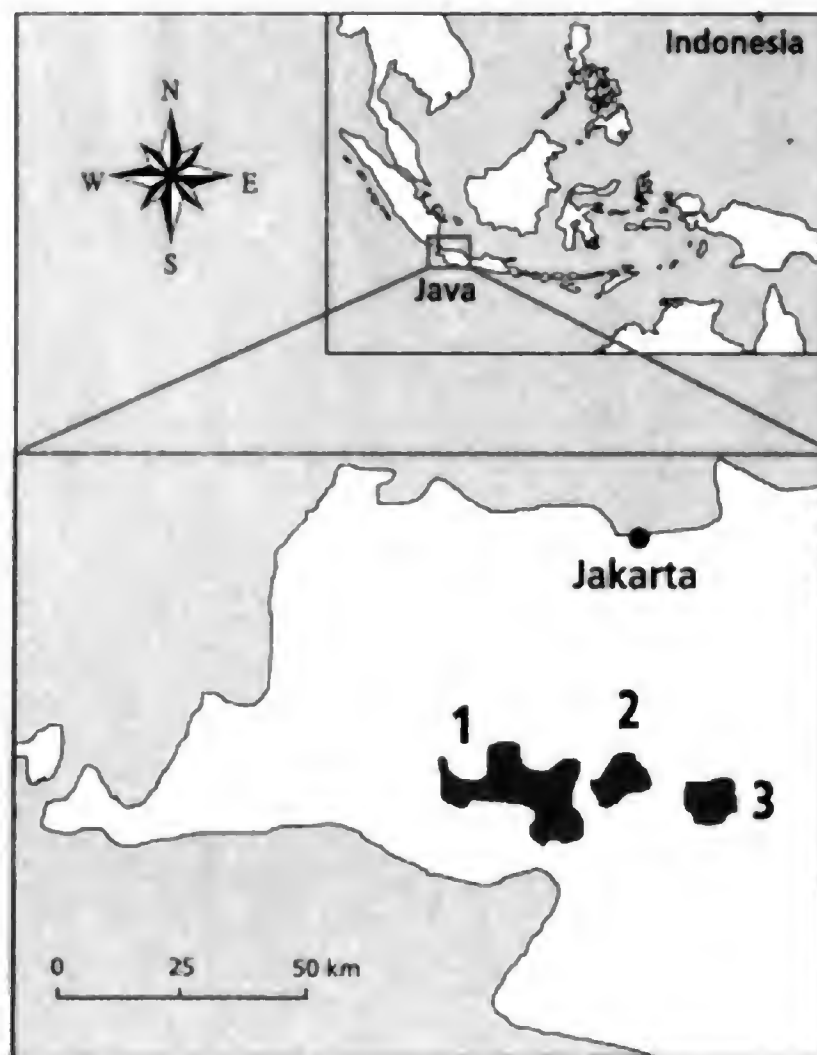


Figure 1. The study areas: 1 = Halimun, 2 = Mt. Salak, 3 = Gede-Pangrango.

status as production forest. Part of the forest, particularly on the lower slopes of the mountain, has been transformed into tree plantations or secondary forests. The lowermost part of the forest, bordering cultivated areas, is used by local villagers for collecting forest products. There are large areas of primary forest present on the mountain, mostly at higher elevations. Mt. Salak has a very high annual rainfall and is an important water-catchment area.

Gede-Pangrango. This national park includes the volcanoes Mt. Gede (2958 m) and Mt. Pangrango (3019 m). It contains 15 196 ha of rainforest (Fig. 1) and includes some of the oldest, protected forests in Indonesia. The annual rainfall is 3000–7000 mm (RePPProT 1990). There is little seasonal variation with only a slight decrease in rainfall from May–August. However, El Nino events (such as in 1997) may result in extended and more pronounced dry seasons, lasting until November. The park consists mainly of montane forest and includes the botanical gardens of Cibodas. The nearby Telaga Warna Nature Reserve surrounds a small lake; the reserve proper covers an area of 350 ha. The total area of this study area is ca. 20 000 ha (van Balen et al. 2000).

Field Observations. *Behavior of territorial pairs.* When weather conditions are favorable, eagles may soar above the forest within their home ranges, and perform territorial displays. Therefore, the birds can be observed from places with a good view of the surrounding terrain. To identify the home ranges of the different pairs, we used

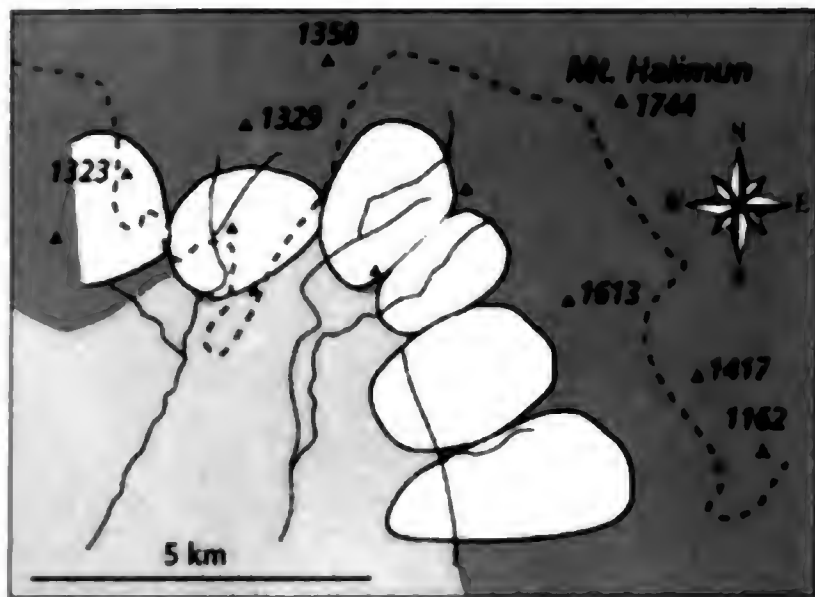


Figure 2. The distribution of Javan Hawk-Eagle home ranges at the southeastern border of Halimun. The home-range sizes were estimated using the distance between centroids of neighboring territories as the diameter of a hypothetical-circular home range. The dashed line denotes the boundary of the national park, the dark gray area represents forest, and light gray area represents open areas. Triangles and numbers = high points and elevation in m.

one of the following criteria: either simultaneous observation of neighboring pairs, individual recognition based on variation in plumage color, or molt pattern. To obtain an estimate of the density of territorial eagles in the area, four observers performed observations along a 10 km stretch of forest edge in the Halimun study area over 9 d during two time periods, 30 August–2 September and 26–30 September 1997. The total observation time was 67 hr. The map of the study area (Fig. 2) is based on maps in Whitten et al. (1996) and from Biodiversity Conservation Project in Indonesia (1997). The border between home ranges was mapped based on observations of territorial display and other flight activity, and the distances between the centroids of the five neighboring territories were measured from the map (Fig. 2).

Distances between nests. In the study areas in Mt. Salak and Gede-Pangrango, we were given the locations of six nests by local inhabitants. Therefore, we were able to measure the distances between nests of neighbor pairs in these areas. For this study, we included three nests which were identified in 1997 in Salak. These nests were plotted on available maps (Bakosurtanal 1997) and the distances between them were measured on the maps. The same method was used on three occupied neighbor nests in Gede-Pangrango in 1998, which were plotted on maps from Bakosurtanal (1990a, 1990b).

Radiotelemetry. An adult Javan Hawk-Eagle male was caught by use of a snare on the nest in Mt. Salak on 19 October 1997, and equipped with a VHF transmitter weighing 25 g (BioTrack Inc., Dorset, U.K.). The transmitter was equipped with a mercury activity switch. It was attached as a backpack by a harness made of Teflon (Bally Ribbon Mills, Bally, PA U.S.A.) ribbon using a Y-type attachment (Buehler et al. 1995). This male was ra-

dio-tracked intensively from five fixed receiver stations from 31 March–15 May 1998 with a four-element yagi hand-held antenna. The coordinates of these receiver stations (locations not differentially corrected) were determined with a GPS receiver (GPS 45, Garmin International Inc., Olathe, KS U.S.A.).

During observations, data were collected every 30-min during a 5–10 min interval. Locations were obtained by simultaneous triangulations from two different stations. The number of locations estimated from each station varied from 2–24/d. The positions were often confirmed by visual observations of the eagle flying or perching. The accuracy of the location estimates is probably reasonable due to the short distances (typically <500 m) from the receiver sites to the eagle and the good overview of the area from overlooks. Two types of behaviors were interpreted from radio signals: long pulse as sitting, short or variable pulse as flying or eating.

We collected 126 locations for this Javan Hawk-Eagle during our fieldwork. Home range was calculated with the minimum convex polygon and fixed kernel methods (Worton 1989) using the software program ArcView and the Animal Movements extension (Hooze and Eichenlaub 2000).

RESULTS

Home Range. *Direct observation of territorial behavior.* In Halimun, we found six pairs of Javan Hawk-Eagle along a 10-km distance of forest edge (Fig. 2). The mean estimated distance between centroids of five neighboring territories was 1.8 km, which gives a hypothetical-circular home-range size of 254 ha (Table 1). One home range in Gede-Pangrango was mapped based on sight observations of eagles. This range was 530 ha, of which 220 ha was forest and the rest was tea plantation.

Distances between nests. In Gede-Pangrango, we found that the distances between three occupied nests from the same year were ca. 3 km, which gives a hypothetical circular home-range size of 710 ha. The distances between three nests occupied the same year in the Salak area were ca. 2 km, resulting in a hypothetical circular home-range size of 314 ha (Table 1).

Radiotelemetry. The home range of the radio-equipped Javan Hawk-Eagle male from 31 March–15 May 1998 was confined within an area of 1.5×2.2 km. It was located at $6^{\circ}40'–6^{\circ}41'S$ and $106^{\circ}44'–106^{\circ}00'E$, and between 620–1550 m altitude (Fig. 3). The home-range size according to the 95%-probability contour of the fixed-kernel method was 289 ha. A minimum-convex polygon around all fixes gave a home range of 310 ha. Hence, we estimated the home range of this eagle at ca. 300 ha (Table 1).

The types of habitat in the home range consisted

Table 1. Home-range sizes estimated by different methods: direct observations of territorial behavior of breeding pairs, distances between nests, and radio-tracking of an adult male.

METHOD	DISTANCE BETWEEN ACTIVITY CENTERS (km) (N)	ESTIMATED SIZE OF HOME RANGE (ha)	STUDY AREA
Distance between home-range centroids	1.8 (4)	254	Halimun 1997
Mapped by sight observations	(1)	530	Gede-Pangrango 1998
Distance between nests	3 (2)	710	Gede-Pangrango 1998
Distance between nests	2 (2)	314	Salak 1997
Mapped by radiotelemetry	(1)	300	Salak 1997

of undisturbed primary forest, production forest (*Pinus* sp.) and disturbed natural forest. Frequent observations of soaring and displaying Crested Serpent Eagle (*Spilornis cheela*), Black Eagle (*Ictinaetus malayensis*), and Changeable Hawk-Eagle (*Spizaetus*

cirrhatius limnaeetus) indicated that the home range of the Javan Hawk-Eagle partly overlapped the home ranges of these eagles.

In Gede-Pangrango, no observations of Javan Hawk-Eagles were made at altitudes over 2000 masl. The six nests were situated between 1200–1400 masl.

Time Budget and Behavior. The time budget data from 75 hr of observations between 0600–1800 H of the radio-tracked male in Salak showed that this Javan Hawk-Eagle spent 42.8% of its time flying or feeding, and 57.2% perching.

DISCUSSION

Home-range Size. When using a hand-held antenna in the field, it is difficult to obtain better than 5 degrees accuracy on the signal bearing. This would result in a 10 m error at a tracking distance of 100 m (Kenward 2001). The outermost fixes were up to 1 km away from the observer, thus involving a potential error of ca. 100 m in the location accuracy. Although we did not test the accuracy of locations, we suggest that some of our location errors may have been compensatory (i.e., one location could have had an error of several hundred meters to the east, while another location could have had an error similar distance to the west. Therefore, even though the accuracy of our telemetry data were limited, we feel that our results provided a reasonable approximation of the home-range size used by one Javan Hawk-Eagle.

Our estimates of home-range sizes of 230–710 ha, suggesting a median value of ca. 400 ha (Table 1) are considerably lower than those given by other authors (Meyburg et al. 1989, Sözer and Nijman 1995, Thiollay and Meyburg 1988), which ranged from 1200–12 000 ha. Madrid et al. (1991) found that the home-range size of the Ornate Hawk-Eagle

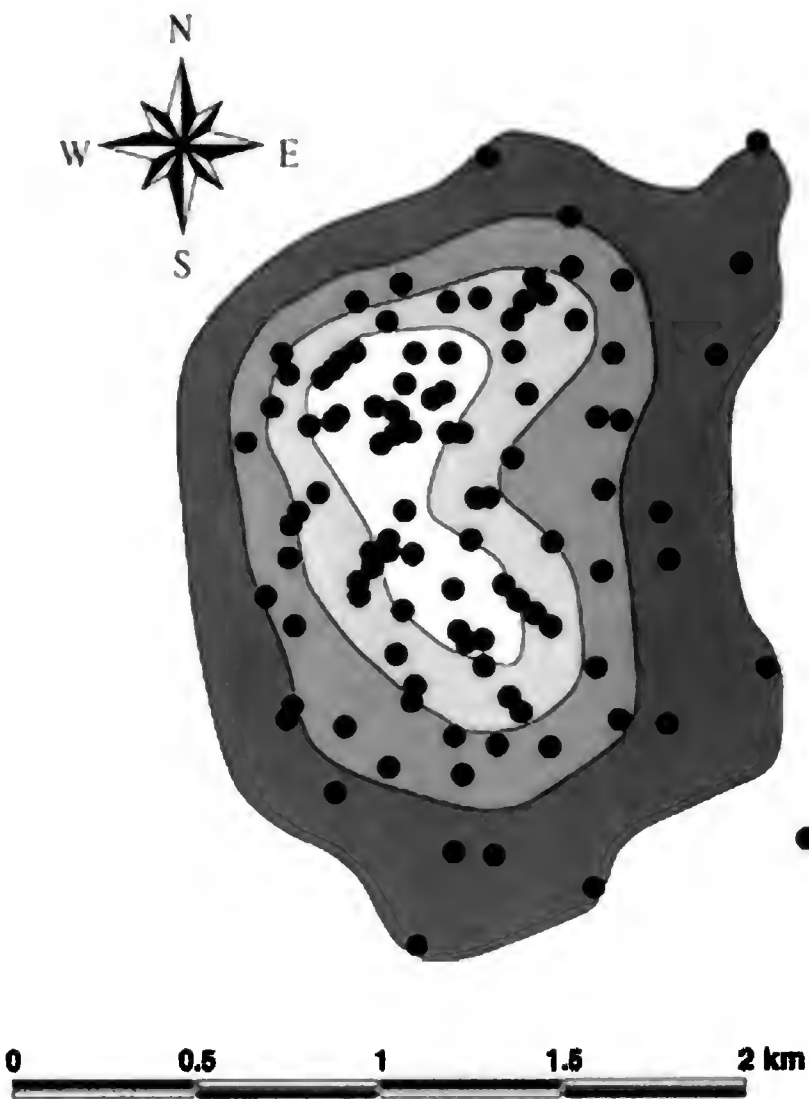


Figure 3. Home range of a VHF radio-equipped adult male Javan Hawk-Eagle in the nonbreeding season. The 95, 75, 50, and 25% probability contours using a fixed-kernel method as shown. The black circles show 126 radiotelemetry locations. A least-square cross validation for the smoothing factor (H) was performed, and its value was set to 200.

(*Spizaetus ornatus*) in Guatemala was 800 ha for males and 1300–2100 ha for females. In the Japanese Mountain Hawk-Eagle (*Spizaetus nipalensis orientalis*), Yamazaki (2000) found that home ranges were normally >2000 ha, (neighbor-nest distances 1.5–5.6 km, \bar{x} = 4 km). The mean density of breeding pairs of this species has been calculated at one pair per 2500–2800 ha uniformly throughout Japan (Yamazaki 2000). A similar home-range size (1270–3230 ha) has been recorded in the Philippine Hawk-Eagle (*Spizaetus philippensis*; Preleuthner and Gamauf 1998). However, relatively small home ranges (ca. 650 ha) have been documented in Crowned Hawk-Eagles (*Stephanoaetus coronatus*; Shultz 2002), and the nearest-neighbor distance between nests averaged 1.8 km. In the huge Harpy Eagle (*Harpia harpyja*), occupied nests have been recorded as close as 3–5 km apart in South and Central America (del Hoyo et al. 1994).

Our results from a single radio-tracked male probably represent the home-range size of a pair. We suggest that the male typically uses the combined home ranges of the male and the female exploited during the breeding season. Our telemetry data were collected about 5 mo after the young left the nest. This use area probably represents the breeding home range, as the juveniles stay with their parents for a year or longer (Nijman et al. 2000). Also, we repeatedly saw territorial interactions between neighboring pairs, suggesting that adjacent home ranges were defended.

In the Halimun area, we observed Changeable Hawk-Eagles, Black Eagles, and Crested Serpent Eagles commonly in the home ranges of Javan Hawk-Eagles indicating home-range overlap among these species (Røv et al. 2000).

Habitat Use. Thiollay and Meyburg (1988) suggested that the Javan Hawk-Eagle was dependent on primary rainforest, although those authors also mention that the species was seen in three degraded forest areas around Bogor. They also stated that hawk-eagles were seen flying over a plantation between two patches of forest as well as perched near a road in secondary forest at Meru Betiri in east Java. Nijman and van Balen (2003) found that the prime habitat for adult Javan Hawk-Eagles were evergreen forest and to a lesser degree secondary forest, and that immatures and juveniles had a greater preference for open woodland (forests with large clearings, small forest fragments, and young tree plantations) than adults.

Our observations suggest that the species uses

both primary and secondary forests for hunting and nesting. We have observed Javan Hawk-Eagles hunting over cultivated areas both in Halimun and Gede-Pangrango with home ranges that included such areas. We did not observe this for our radio-tagged bird in Salak as this home range did not include cultivated sites. When the home ranges are bordering open areas, the eagles may include some of these areas in their home ranges (Nijman and van Balen 2003, Nijman 2004, pers. obs.). However, our observations may be biased because they were made along forest borders. We have observed that the eagles can obtain food opportunistically from outside its primary habitat. This is based on prey remains of Barred Buttonquail (*Turnix suscitator*), an open-habitat species, and shows that some prey must be taken outside the forest. We have also obtained information from local people that domestic chickens have been taken in a village close to a nest of Javan Hawk-Eagle (Prawiradilaga et al. 2000).

Population Status. The number of breeding pairs of this species has been estimated by dividing the area of presumed suitable habitat by assumed home-range size. The Javan Hawk-Eagle normally does not nest above ca. 1400 masl (Nijman et al. 2000, pers. obs.); therefore, we excluded these high altitude areas to estimate population size. In areas such as Gede-Pangrango, the eagles sometimes soared to high altitudes, but they were never seen to be encountered by other conspecifics at these higher elevations. If we use 3 km as a mean home-range diameter for the Gede-Pangrango area, this habitat would provide space for about 20 pairs, which is 2–3 times more than previous estimate of 6–10 pairs (van Balen et al. 2001).

Van Balen et al. (2000) estimated the size of available Javan Hawk-Eagle habitat on all of Java at ca. 5480 km² in 22 forest areas (also see van Balen et al. 2001). Based on this finding and a density estimate of one pair per 2000–5000 ha, they estimated the total population of Javan Hawk-Eagles to be between 137 and 200 pairs (van Balen 1999, Nijman et al. 2000). Our data indicated that this estimate probably was too conservative. Extrapolation of our Gede-Pangrango densities to the entire forest habitat would place the population size between 270–600 (median = 435) pairs. However, we must admit that the accuracy of our home-range estimates are limited and our island-wide population estimate is based on a number of assumptions. Therefore, we recommend more studies to be car-

ried out in different forest habitats in other parts of Java. Nevertheless, the species should still be regarded as endangered; it is threatened by both habitat loss and illegal hunting. Because of this, we urge implementation of the Species Recovery Plan (Sözer et al. 1998) proposed by the Javan Hawk-Eagle Working Group to ensure the future conservation of the species.

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POPULATION STATUS AND REPRODUCTIVE PERFORMANCE OF EURASIAN GRIFFONS (*GYPS FULVUS*) IN EASTERN SPAIN

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ABSTRACT.—The Eurasian Griffon (*Gyps fulvus*) has experienced a measurable increase in population numbers in the Iberian Peninsula and, particularly, in the Castellón province during the last two decades. In Castellón, we have located 18 breeding colonies on a 6670 km² area in 2002. These included two new nesting colonies, expanding the known distribution in the province by 64 km². The breeding success was 0.83 chicks/laying pair, productivity was 0.66 chicks per detected pair, and the percentage of pairs initiating breeding activities was 79.5%. Two variables were included in the logistic model that best explained the probability of raising a chick successfully (type of nest and its interaction with orientation). The probability of nest success increased with nests located inside caves and with nests located on open ledges that were oriented to the south. There was a significant relationship between the distance to the nearest-neighbor nest with the nest success (0 or 1) in the logistic-regression analysis.

We suggest that conservation of native fauna is necessary to maintain the griffon population in the province. The reduction and closure of vulture restaurants in existing range may have also stimulated southward dispersal of griffons searching for new trophic resources.

KEY WORDS: *Eurasian Griffon; Gyps fulvus; breeding success; coloniality; productivity; vulture restaurants; Spain.*

ESTATUS POBLACIONAL Y PARAMETROS REPRODUCTORES DEL BUITRE LEONADO *GYPS FULVUS* EN EL ESTE DE ESPAÑA

RESUMEN.—Durante las últimas dos décadas, el buitre leonado *Gyps fulvus* ha experimentado un considerable aumento de su tamaño poblacional en la Península Ibérica, especialmente en la provincia de Castellón. En esta provincia hemos localizado un total de 18 colonias de reproductivas en un área de 6670 km² en 2002. Dos nuevas colonias de cría no se habían citado previamente, y suponen una expansión de 64 km² de la distribución conocida de la especie en la provincia. El éxito reproductivo fue de 0.83 pollos/huevo, la productividad de 0.66 pollos/pareja y el 79.5% de las parejas iniciaron actividades de reproducción. El modelo logístico que mejor explicó la probabilidad de criar un pollo con éxito incluyó dos variables significativas: el tipo de nido y su interacción con la orientación. Los nidos emplazados en cuevas, así como los ubicados en repisas abiertas orientadas hacia el sur, mostraron mayor probabilidad de éxito. Se encontró una relación significativa en el análisis de regresión logística entre la distancia al nido vecino más próximo y el éxito de cada nido (0 ó 1). Sugerimos que la conservación de la fauna silvestre es necesaria para mantener las poblaciones de *G. fulvus* en Castellón. La reducción y cierre de muladares podría haber estimulado la dispersión de los buitres hacia el sur en busca de nuevos recursos tróficos.

[Traducción de los autores]

The large growth in the Eurasian Griffon (*Gyps fulvus*) population in the Iberian Peninsula has been well documented since the 1970s (Errando et al. 1981, Donazar 1987, Arroyo et al. 1990, Donazar and Fernández 1990). The recent national censuses showed increases in breeding pairs of 135% between 1979–89 and 130% from 1989–99 (Del Moral and Martí 2001). In the Castellón province, this growth has been constant and greater

(>150%) than the national mean (Del Moral and Martí 2001). In spite of this growth, expansion of griffon distribution both on a national and a local level has not occurred (Arroyo et al. 1990, Donazar 1993, Del Moral and Martí 2001). Conspecific attraction to nest places (Sarrazin et al. 1995) seems to be among the causative factors for this pattern.

In this paper, we present results related to the population status, reproductive performance (breeding success and productivity), and range expansion for the Eurasian Griffon in the Castellón

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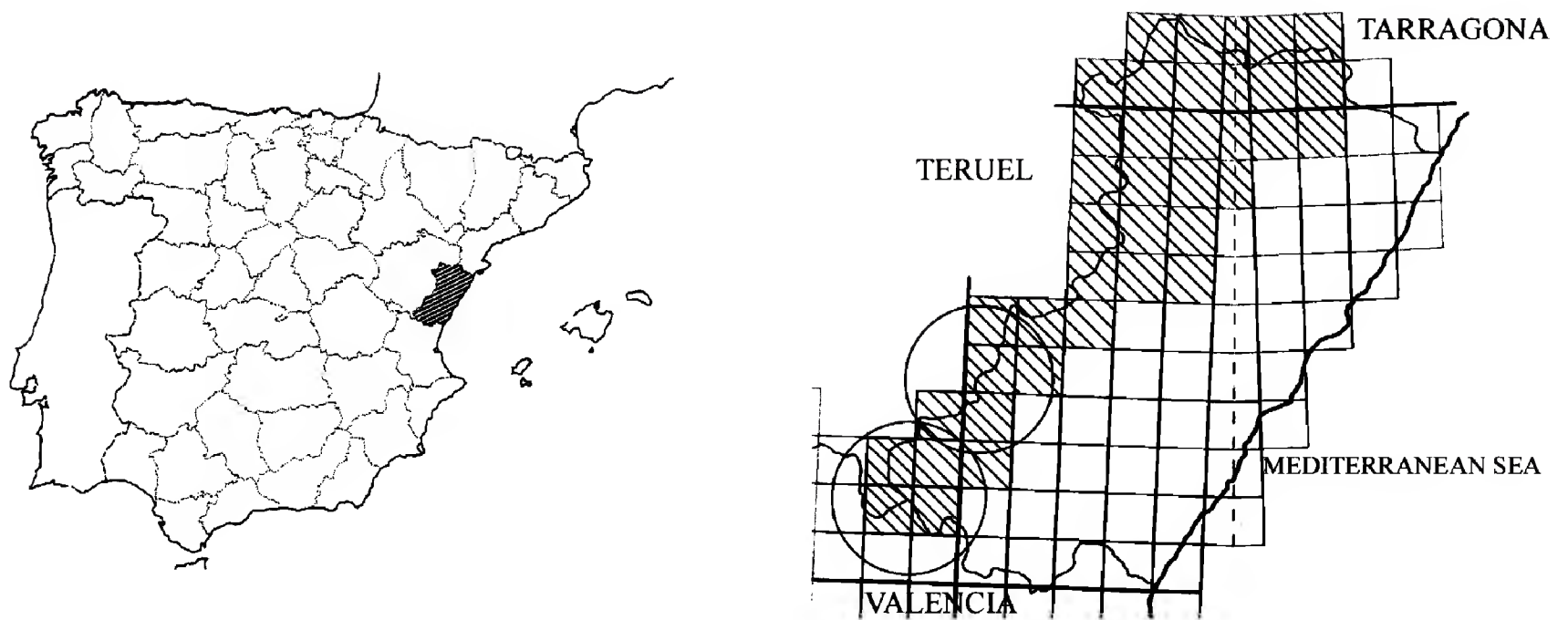


Figure 1. Left: Iberian Peninsula. The shaded area shows the study area, Castellón province. Right: study area general map with Universal Transverse Mercator 10×10 km squares. Shaded area squares show frequent Eurasian Griffon presence. Circles indicate the two new breeding colonies.

province. Age of breeding pairs, type of nest, nest orientations, and distance to nearest conspecific nest were recorded and statistically related to nest success. We also provide an analysis of the physical variables recorded at griffon colonies and their relationship with reproductive performance.

STUDY AREA

The study area comprises the Castellón province (Fig. 1; located in the east of the Iberian Peninsula), including 6670 km^2 ; $40^\circ 47' \text{N}$, $39^\circ 42' \text{S}$, $0^\circ 51' \text{W}$, $0^\circ 32' \text{E}$; $0\text{--}1814 \text{ m}$ above sea level (masl). The area is geomorphologically characterized as the confluence of two mountain ranges: the Iberian system, oriented northwest-southeast on the one hand, and the east-northeast-oriented structures of the Catalánides, parallel to the coastline. This results in a subtabular and a folded-peak line with calcareous material, mostly sedimentary, which supports many cliffs and walls suitable for the nesting of the griffon. Climatologically, it belongs to the Mediterranean area, with an annual mean temperature varying between 17°C in the coast area and 8°C in the inner highlands (where the entire griffon population is located). The annual mean precipitation varies from $400\text{--}900 \text{ mm}$, with maximum values during the fall and minimum values in the summer, characterized by the great interannual irregularity of the Mediterranean weather (Quereda et al. 1999). Bioclimatologically, the study area supports an assortment of vegetation types and ecosystems (Rivas-Martínez 1987). This heterogeneity also manifests itself locally, alternating cultivation zones both irrigated and nonirrigated with forest patches dominated by pines (*Pinus* spp.) and, to a lesser extent, oaks (*Quercus* spp.) and *Juniperus* spp.

The livestock industry in the study area is mainly restricted to intensive feed-lot farms, in which animals are confined and not available to vultures (CAPA 1999). Pasture grazing does occur in the northern regions, the only

area where a griffon population has existed for the last 30 yr (Arroyo et al. 1990, Urios et al. 1991, Del Moral and Martí 2001). The livestock is mainly porcine (92.44%), followed in importance by ovine (3.96%), and bovine (2.35%). The availability and use of wild ungulates as a trophic resource for griffons is unknown. Also in the study area, a small number of “vulture restaurants” are scattered in the central part of the province which are available to griffons. “Vulture restaurants” are traditional places close to villages where shepherds and farmers drop carcasses and serve as supplementary feeding sources for carrion-eating birds.

METHODS

We monitored the reproductive success of 112 breeding pairs from December 2001–June 2002. All areas where breeding by griffons was known were observed, as were cliffs larger than 40 m in height with suitable ledges that could be colonized by nesting vultures (Donazar 1993). For the latter, we monitored 85% of the potential nesting cliffs, thus may have missed an isolated-reproductive pair. The coastal area, which has high human density and is less suitable for nesting vultures, was surveyed less intensively; 60% of the potential nesting cliffs surveyed. In the interior areas, we monitored 98% of the potential nesting cliffs.

Observations were made with a $20\text{--}60\times$ telescope during clear days and $>300 \text{ m}$ from nesting cliffs to avoid disturbance to vultures (Fernández et al. 1996, Olea et al. 1999, Gil-Sánchez 2000). At least three visits, in some cases five, were made to every reproductive colony. A preliminary search was made between 20 December and 10 January, in which nuptial flights and copulations were observed (Donazar 1993). The first visit was made between 16 February and 23 February, in which a sketch of the cliff that hosts the colonies was made, noting the locations of pairs and nests. The second visit was made between 21 March and 3 April to confirm the presence/

Table 1. Physical variables recorded at Griffon Vulture colonies ($N = 16$ colonies).

NAME	DESCRIPTION
Cliff height	Cliff height (m); 1:10 000 digital map.
Distance to top of cliff	Distance (m) from the highest nest to the top of cliff; digitally treated images based on known-length segments previously measured on the field. Recurring measures were only counted once (Olea et al. 1999).
Distance to base of cliff	Distance (m) from the lowest nest to the base of cliff; digitally treated images.
Distance from nearest colony	Distance (m) from nearest colony; 1:50 000 Spanish Army Cartographic Service.
MASL	Mean elevation (m) above sea level; 1:50 000 Spanish Army Cartographic Service.
Distance to nearest nest ^a	Distance (m) to nearest neighbor nest in the same colony; digitally treated images.

^a $N = 82$ nests were measured; we could not obtain an adequate digital picture to measure distances accurately at colony No. 13.

absence of the previously-detected pairs, the existence of new nests, and the newly-hatched chicks. Our third visit took place between 19 April–11 May to monitor the development of previously-detected chicks and the presence of new hatchings. Finally, a fourth visit was made in the period between 21 May and 25 June, when 11 of the 18 known colonies were visited. During this last visit, breeding success was recorded, as was the presence of late broods. Those cliffs where the species was not detected during the first two visits were not visited subsequently (Martínez et al. 1997, Del Moral and Martí 2001).

A pair was considered as a laying pair if it was building a nest, incubating, and the griffons were taking turns in the nest, or if typical pair behavior, such as close contact with mutual preening, was observed (Donazar and Fernández 1990, Blanco and Martínez 1996, Olea et al. 1999). A cliff was considered as a colony if it was occupied by at least two pairs and was at least 1000 m away from its closest neighbor, according to the methodology used in the species' 3rd Spanish National Census (Del Moral and Martí 2001). These criteria were modified for two of the colonies because of the more rugged orography of the terrain and its different abiotic characteristics; at these sites we reduced the nearest-neighbor criterion to 600 m. Information gathered for each nest included its orientation and type of location (open ledge, sheltered ledge, or cave). Orientation was measured on the Valencian Cartographic Institute computer-cartographic database to a 1:10 000 scale. For each pair, age was recorded according to plumage (subadult or adult). Those individuals with brown ruff and non-nacreous bill were considered subadults (Donazar 1993, Blanco and Martínez 1996). The following reproductive laying-pair combinations were found: adult-adult, adult-subadult, and subadult-subadult pairs. Selected physical parameters of cliffs were also derived from the cartographic database (Table 1).

The following reproductive parameters were calculated for each breeding colony and for the entire study area: productivity = fledged chicks/detected pairs; breeding success = fledged chicks/laying pairs (Del Moral and Martí 2001). A chick was considered as fledged if, given

its development level during the last visit, it was older than 70 d (Del Moral and Martí 2001). Based on the locations of nesting colonies, we calculated a minimum convex polygon to estimate the area in the province occupied by breeding Griffon Vultures (Olea et al. 1999)

Statistical Analysis. Descriptive statistics were calculated for the most variables: productivity, breeding success, cliff height, distance to base of cliff, distance to top of cliff, distance from nearest colony, and masl. We used linear regressions (Sokal and Rohlf 1981, Draper and Smith 1998) with productivity and breeding success of each colony as dependant variables to examine the influence of measured variables on reproductive performance. Finally, in order to assess the relationships between a dependant (response) factor (each nest's success: 0 or 1) against the independent (explanatory) categorical predictors: orientation, type of pair, type of nest, and distance to nearest nest, a logistic regression analysis was performed (Sokal and Rohlf 1981, Fernández et al. 1996, Everitt and Dunn 2001). To employ this method, we used the link function in the generalized-linear models procedure of SPSS (1998), where the predicted variable was logistically transformed (Agresti 1990, Everitt and Dunn 2001). We assumed a binomial distribution of errors and each nest was considered as one case. Standard-stepwise backward procedure was used, including all variables and then removing not significant variables by Wald's method (Johnson 1998, McNally 2000). If the Wald statistic was significant then the parameter was included in the model. We selected the last significant model that included the fewest variables. All calculations were made using the SPSS v11.5 (SPSS Inc. 1998).

RESULTS

We located 16 colonies and two isolated nests in the study area, with 89 laying pairs and 112 detected pairs. Productivity was 0.66 chicks per detected pair ($N = 112$) and breeding success was 0.83 chicks per laying pair ($N = 89$). The mean number of visits per colony was 3.22 (SD = 0.88,

Table 2. Generalized linear models for nest success (0 or 1) of Eurasian Griffon, using binomial error and logistic links. Significant model ($\chi^2 = 25.33$, $df = 14$, $P = 0.03$, $R^2 = 0.25$) involved type of nest and its interaction with orientation.

	β	STANDARD ERROR	WALD	P
All nests			7.37	0.03
Sheltered ledge	-2.37	1.02	5.43	0.02
Open ledge	-1.96	0.88	4.93	0.03
Nest by orientation			7.95	0.79
Sheltered ledge toward north	21.20	17 974.84	0.00	0.99
Sheltered ledge toward northeast	21.20	17 974.84	0.00	0.99
Sheltered ledge toward east	1.61	1.37	1.39	0.24
Sheltered ledge toward southeast	21.20	16 408.71	0.00	0.99
Sheltered ledge toward south	21.20	12 118.64	0.00	0.99
Sheltered ledge toward southwest	21.20	23 205.42	0.00	0.99
Sheltered ledge toward west	21.20	16 408.71	0.00	0.99
Open ledge toward northeast	20.80	15 191.52	0.00	0.99
Open ledge toward east	20.80	20 096.49	0.00	0.99
Open ledge toward south	2.13	0.88	5.86	0.01
Open ledge toward southwest	1.32	0.81	2.66	0.10
Open ledge toward west	0.51	1.06	0.23	0.63
Constant	2.37	0.60	15.37	<0.01
Residual deviance	105.57			

$N = 58$). The percentage of pairs initiating reproduction was 79.46%. The number of pairs per colony ranged from 2–18 ($\bar{x} = 6.88$, $SD = 5.45$, $N = 16$).

All the colonies were located on cliffs over 40 m high ($\bar{x} = 131.67$ m, $SD = 74.06$, range = 40–320 m), between 645 and 1150 masl ($\bar{x} = 850.56$, $SD = 139.80$). The mean distance from nearest colony was 5523.72 m ($SD = 7743.66$, range = 325–24 000 m). The mean distance from the highest nest to the top of cliff 32.45 m ($SD = 31.11$, range = 10–120 m), and the distance from the lowest nest to the base of the cliff was 43.45 m ($SD = 24.91$, range = 10–80 m).

The location of the nests was as follows: open ledge, 55 nests; sheltered ledge, 26 nests; cave, 19 nests ($N = 100$). The nest orientations were mostly south (33.33%, $N = 33$) and southwest (25.25%, $N = 25$). Breeding pairs were comprised of: adult-adult (24.11%, $N = 27$), at least one adult (28.57%, $N = 32$), adult-subadult (8.93%, $N = 10$), at least one subadult (4.46%, $N = 5$), subadult-subadult (1.79%, $N = 2$), and unknown age (32.14%, $N = 36$). The mean distance to the nearest nest inside the colony was 72.93 m ($SD = 99.54$, range = 4–498 m).

Our results indicated that the nesting distribu-

tion of griffons in Castellón province has expanded in recent years. The species now occupies two new nesting colonies located 41 and 64 km southwest from the previously-reported distribution in 1999 (Del Moral and Martí 2001), which implies an increase of 64 km² (Fig. 1).

No statistical relationship was found between the cliff variables (Table 1) and productivity or breeding success for each colony. There was a significant relationship between the distance to nearest-neighbor nest and nest success in the logistic regression analysis ($P = 0.014$).

Using nest-site characteristics, two significant variables were involved in the model that best explained the probability of breeding successfully: type of nest and its interaction with orientation (Table 2). The probability of nest success decreased with nests located on open ledges and on sheltered ledges, and increases in success with nests inside caves. Also those nests located on open ledges and oriented to the south had a greater probability of producing a chick.

DISCUSSION

The number of nesting colonies in the Castellón province has increased from 14 in 1999 (Del Moral and Martí 2001) to 18 in 2002. However, the num-

ber of isolated pairs decreased from five to two. Productivity (0.66 chicks/pair) and breeding success (0.83 chicks/laying pair) were lower and higher, respectively, than that observed in 1999 (productivity = 0.80, breeding success = 0.81). These small differences could be due to a more thorough monitoring of the population in 2002, with a mean of 3.6 visits per colony compared to 2.6 visits made during the last census. More complete monitoring may have allowed for the detection of a greater number of nest failures (Martínez et al. 1997).

We could not make direct comparisons of reproductive parameters among regions because of different methodologies (Donázar et al. 1988, Arroyo et al. 1990, Leconte and Som 1996, Martínez et al. 1997, Olea et al. 1999). However, the breeding success found in the Castellón province (0.83 chicks/laying pair) was similar to that estimated for the Cantabrian Mountains (0.84; Arroyo et al. 1990) and for the Navarre pre-Pyrenees (0.86; Donázar et al. 1988). Also, the breeding success estimated during this study was higher than the breeding success found in the Spanish Pyrenees (0.77; Arroyo et al. 1990), French Pyrenees (0.76; Leconte and Som 1996), and the Hoces del Duratón (0.63–0.68; Palacín et al. 1993). The productivity in the study area (0.66 chicks/detected pair) was close to that reported for other Spanish territories (e.g., Extremadura = 0.67, Murcia = 0.64, Euskadi = 0.67) and was also near the national mean (0.69; Del Moral and Martí 2001).

The expansion of the species' distribution toward the southwest of the previously known range in the province (Del Moral and Martí 2001) was documented during this study. The two new colonies were probably established recently, and we found the southernmost one in 2002. This area was surveyed exhaustively for the Peregrine Falcons (*Falco peregrinus*) over the past 20 yr (Verdejo 1991, 1994, Gil-Delgado et al. 1995) and no griffon colonies were detected previously. These two new colonies, along with the previously-documented colonies, lie geographically in the western and northern portions of the province (Fig. 1). This distribution corresponds with lower human-density zones where the agrarian and livestock-related activity is still present (CAPA 1999, García-Rippolés et al. 2004). We suggest that this southward expansion may aid in the species' recovery and compensate for those locations where the species was extirpated, such as the northern portion of Valencia province (Urios et al. 1991). It is notable that

91.66% of the reproductive individuals in the two new colonies are adults ($N = 11$ pairs). Only one breeding pair formed by subadult-plumage individuals was recorded and they failed in their nesting attempt. This proportion matches that recorded in a northern region of Spain in a 1997 (Olea et al. 1999), where 92% were adults ($N = 38$).

The percentage of adults composing breeding pairs (61.61%, $N = 69$) in the study area was lower than that of other Spanish peninsular territories such as the West Pyrenees (75%), the Castilla Meseta (72.2%), Extremadura (72.7%), and Cádiz (73.1%; Blanco and Transverso 1996). We also noted the low proportion of two-subadult breeding pairs (1.79%) was only comparable to Castilla Meseta (3.3%; Blanco and Transverso 1996).

Our results from the logistic-regression analysis showed that the probability of raising a chick was related to the type of nest and its orientation. Age of breeding pairs was not related to the probability of nest success. To a lesser extent, the logistic model indicated a positive relationship between south-oriented nests located on open ledge and the probability of success. In our study area, this may have resulted in a higher probability of success because these sites were less exposed to the Mediterranean winter and thus, inclement weather. For the same reason, as was suggested by Elosegui (1989), nests located in caves probably had a higher probability of supporting a successful nest. Nevertheless, Donázar (1993) argued that there was generally no preference for a specific nest orientation by griffons, and that patterns observed were likely dictated by mountain range orientation.

The Eurasian Griffon is mostly a colonial nesting bird (Cramp and Simmons 1980, Donázar 1993). This likely is related to the spatial distribution of the species' food resources (Horn 1968, Donázar 1993). The unpredictable nature of the availability of carrion has been proposed as the main factor favoring this behavior (Donázar 1993). In our study, this was supported by the negative relationship observed between the distance to the nearest neighbor nest in the same colony and its success. We suggest that the carrion availability in our study area was unpredictable, and that the number of permanent functioning "vulture restaurants" were few. This unpredictability of food resources may explain why these colonies exhibiting greater nest aggregation have the highest reproductive performance in our province. We suggest that the colonies might act as effective information centers

(Ward and Zahavi 1973). In addition, the colonial habit could also reduce the predatory risk by Common Ravens (*Corvus corax*; Elosegui 1989).

Factors like the increasing of livestock-trophic resources, the recovery of wild fauna, the creation of vulture restaurants, and the lessening of direct and indirect prosecution of the species by humans in recent years (Donazar 1993), probably has fostered the species' range expansion. Moreover, due to "mad-cow" disease in Europe in 1999 (García-Ripolés et al. 2004), the National Spanish Government prohibited the *ad hoc* dumping of carcasses in an attempt to prevent any possible effects on scavengers. New national laws concerning the establishment of "vulture restaurants," and successive cases of livestock diseases, might have eliminated the access to previously available food resources to carrion-eating birds. This reduction in food availability may have helped to stimulate southward range expansion by Eurasian Griffons in the Castellon province.

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SHORT COMMUNICATIONS

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GENDER DETERMINATION IN THE SWAINSON'S HAWK (*BUTEO SWAINSONI*) USING MOLECULAR PROCEDURES AND DISCRIMINANT FUNCTION ANALYSIS

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KEY WORDS: *Swainson's Hawk*; *Buteo swainsoni*; gender determination; molecular sexing; morphometric measures; wintering grounds.

Gender identification of individuals is important in many studies of wild animals. However, easy determination of sex is difficult for monomorphic species including most birds of prey. Many raptor species show little plumage dimorphism, and although females are generally larger than males, overlap in morphometric measurements and body mass make gender determination difficult even when birds are captured and handled.

The Swainson's Hawk (*Buteo swainsoni*) breeds in North America and migrates to southern South America during the boreal winter that involves a trip of ca. 10 000 km each way (second longest migration distance among raptors; England et al. 1997, Fuller et al. 1998). Male and female Swainson's Hawks are similar in plumage when adults (Wheeler and Clark 1995, England et al. 1997), and as in most of the genus *Buteo*, plumage polymorphism occurs both in immature and adult birds. Although accurate methods for gender determination using morphometric data have been developed for several raptor species (Bortolotti 1984a, 1984b, Garcelon et al. 1985, Edwards and Kochert 1986, Ferrer and De Le Court 1992, Balbontín et al. 2001, Palma et al. 2001), no reliable criteria for gender determination of Swainson's Hawks using external characteristics have been described.

During the last decade, the development of laboratory techniques involving molecular procedures has provided reliable methods for the accurate gender determination of the majority of avian species (Ellegren and Sheldon 1997). PCR-based methods targeting CHD1-Z and CHD1-W genes are purported to be of universal application to birds, with the exception of ratite species (Ellegren 1996, Fridolfsson and Ellegren 1999). The aim of this study was to develop an accurate method for gender determination of Swainson's Hawks using molecular procedures and

morphometric criteria. Our goal was to obtain a general model, derived from discriminant analysis, to determine gender of immature and adult Swainson's Hawks.

METHODS

We captured and sampled free-living Swainson's Hawks during two wintering seasons (austral summers) in three study areas located in central Argentina. We captured 34 hawks in the vicinity of a roost site near Las Varillas, Córdoba province (31°58'S, 62°50'W), from 19–26 January 2003. One hawk was captured in northern La Pampa province (35°14'S, 63°57'W) on 21 November 2002, and 34 hawks from 7–10 December 2003 at the same site. The sample was completed with 35 hawks captured near Santa Rosa (36°33'S, 64°07'W), La Pampa province, from 21–29 January 2004. The habitat where trapping was conducted consisted of agricultural fields of continuous crops, with soybeans as the principal crop. Planted pastures and natural fields comprised the remaining habitat.

Hawks were captured in open fields near the roost using bal-chatri traps (Berger and Mueller 1959) in early morning and during the afternoon. Traps were set in front of fence posts usually used by hawks for perching, both when they left roosts in the morning and during late afternoon before returning. Captured hawks were aged as juveniles or adults based on plumage characteristics (Wheeler and Clark 1995), with immature birds grouped with juveniles using the same criteria employed by Goldstein et al. (1999). Hawks were banded and weighed with a 1500 g Pesola scale (Pesola AG, Baar, Switzerland) to the nearest 2 g. Six morphometric measurements were taken from adults and juveniles. We measured the length of wing chord (WING) and tail (TAIL) using a plastic rule to the nearest 1 mm, and length of the exposed culmen (CULMEN), tarsus (TARSUS), and hallux claw (HALLUX) using a caliper to the nearest 0.05 mm. We also measured the forearm length (FORE-ARM), or the length from the front of the folded wrist to the proximal extremity of the ulna, also using a caliper (Ferrer and De Le Court 1992, Balbontín et al. 2001; Fig 1). For a few birds only some of the body measurements were recorded (Tables 1, 2).

Approximately 2 ml of blood were taken from each bird from the brachial vein. The blood was placed in tubes with 96% ethanol that were kept in coolers until analysis in the laboratory. The cellular fraction of the

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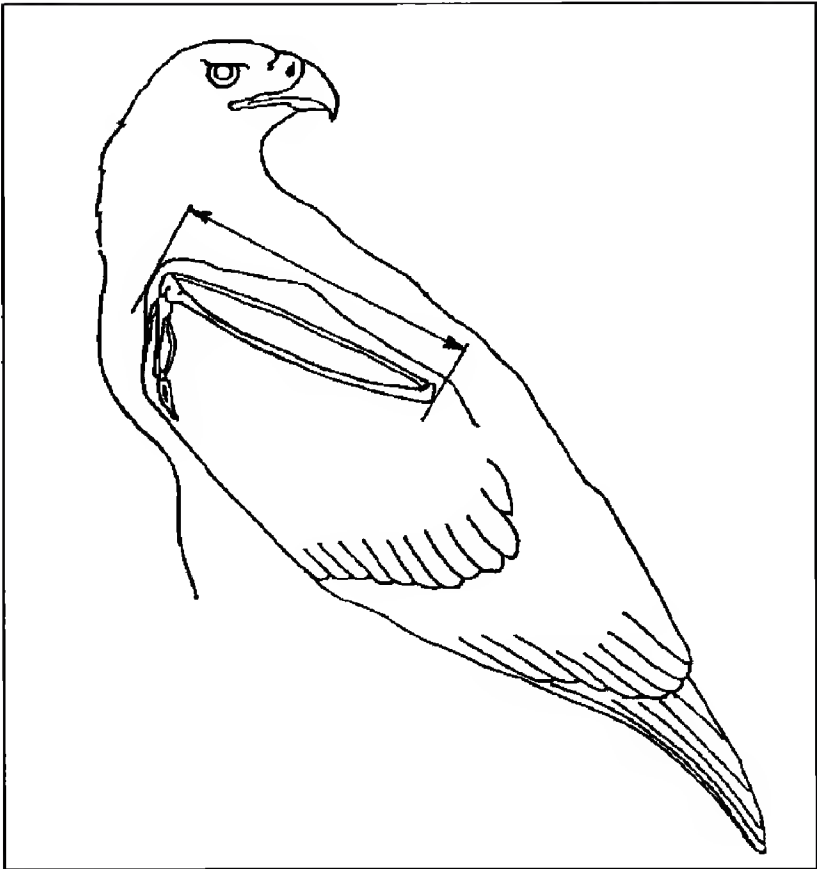


Figure 1. Measurement of forearm length in Swainson's Hawk.

blood sample was used to determine gender for all hawks. For this analysis, we used primers 2550F (5'-GTTACTGATTCGTCTACGAGA-3') and 2718R (5'-ATTGAAATGATCCAGTGCTTG-3') to amplify the W chromosome gene following Fridolfsson and Ellegren (1999; Fig. 2).

We performed multivariate analysis of variance (MANOVA) followed by univariate analysis of variance (ANOVA) to check for differences in morphometric measures among age and sex classes (Zar 1996). Sexes were discriminated with a stepwise discriminant analysis. We used a cross-validation (also called Jackknife) procedure to assess the predictive power of the discriminant functions, in which each individual was classified using a function derived from the total sample less the individual being classified (Manly 1986). Cohen's Kappa statistic was also

calculated and significance tests were performed for each of the resulting discriminant functions. This statistic estimates the correct classification rate adjusted by chance, considering also the effect of unequal group sizes in the probability of correct classification (Titus and Mosher 1984).

RESULTS

The total sample analyzed included 66 males (32 juveniles and 34 adults) and 38 females (17 juveniles and 21 adults). Juvenile and adult Swainson's Hawks differed significantly in overall size (MANOVA, $F = 3.21$, $df = 7$, 93 , $P < 0.01$). An ANOVA for each morphometric variable indicated that the difference was primarily due to body mass, culmen, and hallux length differences between adult and immature hawks, while there were no significant differences in the remaining measurements (Table 1). MANOVA test also showed differences between males and females ($F = 35.8$, $df = 7$, 93 , $P < 0.001$). Univariate analysis of variances showed males being significantly smaller than females for all measures (Table 2). The ranges for the six variables were overlapping between gender groups in all cases.

Due to age-related differences in some of the morphometric measures, and in order to obtain a general method to individualize male and female hawks independently of age, we excluded body mass, culmen, and hallux length from the discriminant analysis and considered only those morphometric measures that did not differ between age groups. Discriminant function analysis using single measurements showed that most of the variables were good predictors of gender (Table 3), but every variable considered separately failed to classify 100% of the individuals in the sample correctly. Forearm was the best predictor variable considering the percentage of cases correctly classified and the value of Cohen's Kappa, with a resulting standardized linear function equal to $D_1 = 0.49 \text{ FOREARM} - 69.85$. The function assigned all but 11 individuals to the correct sex after cross-validation (four males and seven females, overall success 89.4%), where values of $D > 0$ identified females and values of

Table 1. Morphometric measurements of juvenile (includes immatures or second year hawks) and adult Swainson's Hawks and analysis of variance (ANOVA) results for age class differences. All measurements, except mass (g) are in mm.

	JUVENILES				ADULTS				ANOVA	
	\bar{x}	SD	RANGE	N	\bar{x}	SD	RANGE	N	F	P
Wing	390.0	16.0	350.0–420.0	49	395.0	16.0	370.0–430.0	55	3.21	0.07
Tail	201.0	12.0	180.0–230.0	49	202.0	11.0	180.0–220.0	55	0.17	0.68
Culmen	22.5	1.3	20.3–25.6	48	23.3	1.2	20.5–26.1	54	8.55	<0.01
Tarsus	70.8	4.5	60.3–79.4	49	70.5	3.8	64.2–80.1	54	0.08	0.77
Hallux	23.9	1.3	21.4–26.7	49	24.5	1.2	22.3–28.1	55	5.63	<0.05
Forearm	136.9	6.2	124.0–149.0	49	138.4	7.1	127.0–157.0	55	1.47	0.22
Mass	759.7	116.7	540.0–1100.0	48	824.8	110.9	580.0–1110.0	55	8.40	<0.01

Table 2. Morphometric measurements of Swainson’s Hawks in wintering grounds and analysis of variance (ANOVA) test results for gender differences. All measurements except mass (g) are in mm.

	FEMALES				MALES				ANOVA	
	\bar{x}	SD	RANGE	<i>N</i>	\bar{x}	SD	RANGE	<i>N</i>	<i>F</i>	<i>P</i>
Wing	409.0	11.0	390.0–430.0	38	383.0	11.0	350.0–420.0	66	127.74	<0.001
Tail	211.0	9.0	180.0–240.0	38	195.0	8.0	180.0–230.0	66	88.98	<0.001
Culmen	24.1	1.1	21.0–26.1	37	22.3	1.0	20.3–25.6	65	69.53	<0.001
Tarsus	72.6	4.0	64.6–80.1	37	69.5	3.8	60.3–78.4	66	15.68	<0.001
Hallux	25.3	1.1	22.6–28.1	38	23.7	1.0	21.4–26.4	66	55.97	<0.001
Forearm	144.2	4.8	134.5–157.0	38	134.0	4.3	124.0–144.8	66	122.68	<0.001
Mass	895.1	118.3	590.0–1110.0	38	735.6	66.8	540.0–880.0	65	76.64	<0.001

$D < 0$ identified males. The dividing point between genders for forearm length obtained by solving for 0 was 140.2 mm, with values over this point representing females and values under it representing males. Forearm, tail length, and wing chord length were retained in the stepwise discriminant analysis. The resulting linear function ($D_2 = 0.36 \text{ FOREARM} + 1.36 \text{ TAIL} + 1.04 \text{ WING} - 120.95$) increased our predictive power against D_1 (Table 3) and a lower value of Wilk’s lambda indicated that females and males were better separated with this linear combination of variables than using only forearm.

DISCUSSION

Our data indicated that there were significant differences between male and female Swainson’s Hawks. However, there was considerable overlap in the ranges of the morphometric measurements, suggesting that the use of relative size as the only criterion to determine gender in this raptor would result in errors.

Bill depth, toe-pad length, and body mass are morphometric measurements frequently used in determining gender of size-dimorphic birds of prey (Bortollotti 1984a,

1984b, Garcelon et al. 1985, Edwards and Kochert 1986). Forearm length is a body feature traditionally not recorded for wild raptors, but its use has become more common as it is a measure easily obtained from museum skins. Furthermore, it has been shown to be a low variance measure with high repeatability among observers (Ferrer and De Le Court 1992). These features make forearm a reliable morphometric measure that should be considered as a general and standard measure in morphometric gender determination of birds of prey.

Ideally, a technique for gender determination would be applicable to individuals of all ages and under different conditions. Our model based on forearm as a single explanatory variable can be used even on birds showing incomplete molt or evidence of loss of corporal mass due to fasting. The alternative model (D_2) can be also applied in cases in which loss or gain of body mass is suspected to occur (see Smith et al. 1986, Goldstein et al. 1999). The second function, which classified the highest percentage of cases after the cross-validation and chance correction tests, produced a better separation of groups (lower value of Wilk’s lambda), but needed more vari-

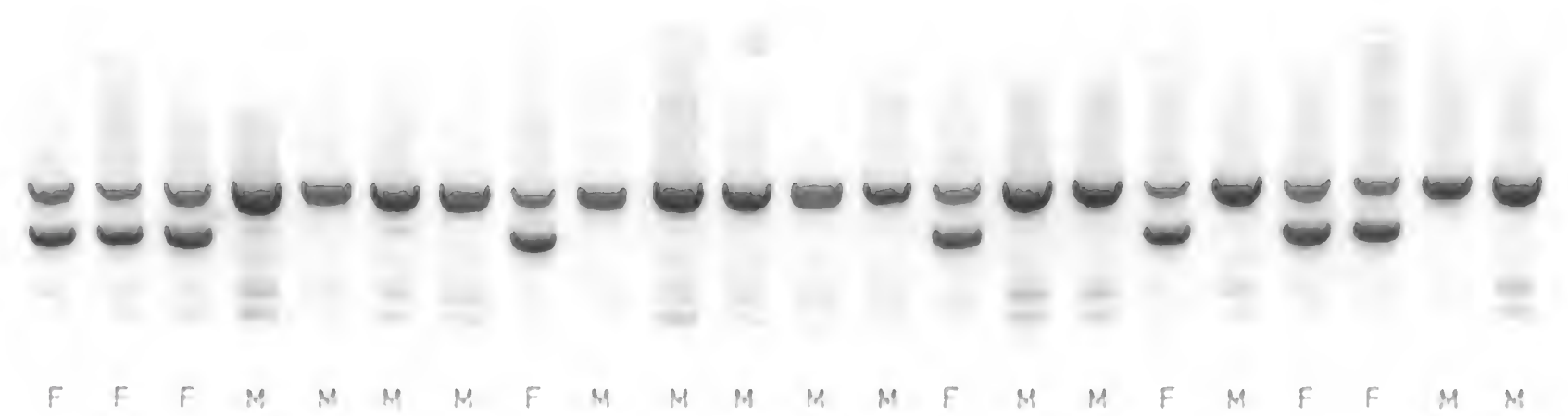


Figure 2. Gender determination using PCR methods. A multiple amplification with 2550F amplify a 420 bp fragment of W chromosome in females and 2550F + 2718R that amplifies 600 bp fragments in both sexes. Males and females are indicated as M and F, respectively.

Table 3. Accuracy of sexing Swainson’s Hawks obtained from discriminant analysis using single measurements or combinations of morphometric variables, and assessed by cross-validation procedure and Cohen’s Kappa calculation. Single variables are ordered from higher to lower values of Cohen’s Kappa.

VARIABLE	CASES CORRECTLY SEPARATED					COHEN’S KAPPA	P
	WILK’S LAMBDA	N	PERCENT FEMALES	PERCENT MALES	PERCENT OVERALL		
Forearm	0.454	(104)	81.6	93.9	89.4	0.77	<0.01
Wing	0.444	(104)	81.6	90.9	87.5	0.73	<0.01
Tail	0.534	(104)	81.6	90.9	87.5	0.73	<0.01
Tarsus	0.866	(103)	70.0	87.5	82.4	0.28	>0.05
Forearm + Tail + Wing	0.332	(104)	86.8	97.0	93.3	0.85	<0.01

ables to be applicable. Its use would be better when complete data sets of the variables are available and given that measurements are not biased by external factors (e.g., molting). Furthermore, D_1 discriminant function allows for gender determination of dead birds when natural decomposition and the effect of scavengers after days of exposure in the field makes classification of sex by standard forensic methods impossible.

Insecticide poisoning of hawks in their wintering ground during 1995–96 and 1996–97 austral summers (Woodbridge et al. 1995, Goldstein et al. 1996) has been documented in this species, with ca. 20 000 birds poisoned in 1996–97. Gender determination of Swainson’s Hawks would provide a valuable tool for a complete assessment of these mortality incidents, including the gender of affected birds.

RESUMEN.—*Buteo swainsoni* es un ave de presa poco dimórfica, y aunque las hembras suelen ser más grandes que los machos, la determinación del sexo en esta especie puede ser difícil, aún cuando las aves son capturadas y manipuladas. En este artículo presentamos un método de sexado para *B. swainsoni* basado en técnicas moleculares y análisis discriminantes. Los datos empleados corresponden a medidas morfométricas de 104 individuos silvestres capturados en el área de invernada de la especie durante los veranos australes 2002–03 y 2003–04. Encontramos diferencias significativas entre machos y hembras en todas las medidas morfométricas consideradas, mientras que los juveniles se diferenciaron de los adultos sólo en su masa corporal, la longitud del culmen y la longitud del hálux. Usando sólo la longitud del antebrazo como variable de predicción, nuestra función discriminante clasificó correctamente el 89.4% de los machos y el 93.9% de las hembras. Una segunda función que incluía la longitud del antebrazo, de la cola y de la cuerda alar mejoró la separación de los grupos y también el porcentaje de individuos correctamente clasificados (97.0% y 93.3% de los machos y hembras, respectivamente). El uso de medidas relacionadas con el tamaño estructural de las aves como la longitud del antebrazo,

de la cola y del ala hacen de éste un método seguro y de amplia aplicación, aún para aves pertenecientes a distintas clases de edad.

[Traducción de los autores]

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PRODUCTIVITY AND FLEDGLING SEX RATIO IN A CINEREOUS VULTURE (*AEGYPIUS MONACHUS*) POPULATION IN SPAIN

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Upon initial review, the mechanism of chromosomal gender determination in birds and mammals seems to be a factor limiting the parents' ability to modify the sex ratio of their progeny (Charnov 1982). However, sex allocation theory (Fisher 1930, Charnov 1982) predicts that the sex ratio can deviate from the expected 1:1, particularly when the costs of rearing the two genders are

different. The optimal sex allocation for individuals can be predicted from three basic non-mutually exclusive hypotheses (reviewed by Frank 1990). (1) Fisher (1930) proposed that parental expenditure in the population should be equal for all sons and daughters, which would result in a population sex ratio biased toward the gender that costs less to produce. (2) Trivers and Willard (1973) hypothesized that if the reproductive return differs between genders depending on parental condition at the time of breeding, natural selection would favor facultative adjustments of offspring sex ratios to obtain the maximum fitness from a breeding attempt. (3) Charnov (1982) generalized Trivers and Willard's hypothesis to cover any socio-environmental variable that might pre-

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dictably affect the fitness of sons and daughters unequally

Biases in the fledgling sex ratio may reflect an adaptive manipulation by the parents, by mechanisms that are not clearly understood (Krackow 1995). Otherwise, they may arise from nonadaptive mechanisms such as gender differences in chick survival rate between hatching and fledging (Clutton-Brock et al. 1985, Arroyo 2002) due to the parents' inability to rear the more costly sex.

In raptors, as in other groups of birds, some reproductive parameters may reflect the environmental or parental conditions during the breeding season (Dawson and Bortolotti 2000). For instance, a decrease in food intake due to the parents' low foraging efficiency or reduction in food availability may be reflected in such reproductive variables as clutch size (Corbacho et al. 1997) or productivity (Corbacho and Sánchez 2000, Dawson and Bortolotti 2000). Therefore, interannual variations in population productivity may be good indicators of any environmental stresses affecting the birds. This is especially true in Mediterranean environments, where the harsh and highly-variable conditions of summer are a major constraint on reproduction (Corbacho and Sánchez 2000, Costillo et al. 2002a).

Recent empirical studies on raptors have provided evidence for the existence of significant biases in the sex ratio of the progeny depending on the environmental and social conditions experienced by the parents during the breeding season (e.g., Dzus et al. 1996, Appleby et al. 1997, Post et al. 1999, Korpimäki et al. 2000, Byholm et al. 2002, Hipkiss et al. 2002). Most of these studies have focused on species with marked sexual dimorphism in size. In such cases, one can predict that a bias in the sex ratio, whether adaptive or not, will arise as a result of the difference in energy requirements or in vulnerability to adverse conditions between male and female chicks (Torres and Drummond 1997, Arroyo 2002). There have been fewer studies of variations in the nestling sex ratio in species that are monomorphic or have only slight sexual dimorphism (Cooch et al. 1997, Sheldon et al. 1998, South and Wright 2002). The main limitation has been the difficulty of assigning gender to the chicks of these species. However, the advances in molecular techniques in the last decade allow the relatively easy and accurate gender determination of a wide survey of bird species (Ellegren 1996).

The Cinereous Vulture (*Aegypius monachus*) is a large raptor widely distributed throughout the western Palearctic. Except for in the Iberian Peninsula, its populations have been greatly reduced (Cramp and Simmons 1980, del Hoyo et al. 1994). This species is of conservation concern, being classified as near-threatened worldwide (Collar et al. 1994) and as vulnerable in Europe and Spain (Blanco and González 1992, Tucker and Heath 1994). Knowledge of its basic ecology, including aspects related to reproduction, is therefore of great importance for the conservation of the species.

Here, we report the patterns of variation in productivity and fledgling sex ratio in a Cinereous Vulture population in Spain during 3 yr. We analyze whether the inter-year variations in breeding success had any relationship to fledgling sex ratio or on the fledglings' nutritional condition. Also we examined whether there were differences in nutritional condition between the genders that may favor manipulation of the sex ratio in this species under certain conditions.

There are two fundamental aspects in which this species differs from other raptors related to studies of sex ratio. Firstly, its sexual dimorphism is only slight, females are larger than males (Donazar 1993). Secondly, clutches are always composed of a single egg (Cramp and Simmons 1980).

STUDY AREA AND METHODS

The study was carried out in 1998–2000, in the Sierra de San Pedro (Extremadura, southwestern Spain). This area and the region of Extremadura in general, support the most numerous populations of Cinereous Vultures in the Palearctic and those that have experienced the greatest growth in Spain in recent decades (González 1990, Tucker and Heath 1994, Sánchez 1998, Costillo et al. 2002b).

At the beginning of each breeding season (February–March), the entire area was surveyed to determine whether pairs were present. Then nesting attempts were monitored periodically during the breeding season to determine which pairs laid a clutch (Breeding Pairs), and how many reared a chick to fledging (Costillo et al. 2002a). As a measure of reproductive success we used the productivity, estimated as the number of fledglings produced per monitored pair. The population's annual productivity was used as an indicator of the breeding conditions that the individuals experienced in the study area.

A variable number of chicks (11–26) were captured in the nests and their blood sampled each year at 45–60 d of age. Assuming that the same pair reused the same nest in successive years (Cramp and Simmons 1980), we selected 12 nests to monitor during the three breeding seasons. In five nests, we were able to sample a chick each year. In the other seven, either the pair did not lay in one of the years, or the chick did not survive long enough to be sampled. In total, blood from 57 chicks was sampled during the study period, 29 of them belonged to one of the selected family groups.

The blood sample was drawn from the brachial vein using 2 ml syringes and disposable needles. A small part (50 µl) was collected in a capillary tube and transferred to a tube with ethanol. For the remaining sample, plasma was obtained by centrifuging at 8000 g for 10 min, and stored at –20°C. We determined the sex of the chicks using polymerase-chain reaction (PCR) amplifications of the CHD genes (Ellegren 1996). Blood was boiled in NaOH 100 mM for 10 min at 100°C before being added to the PCR reaction. PCR protocols were modified from Fridolfsson and Ellegren (1999). We used the primer set 2552F–2781R, scoring one band in males and two bands in females in a 2% agarose-gel stained with ethidium bromide.

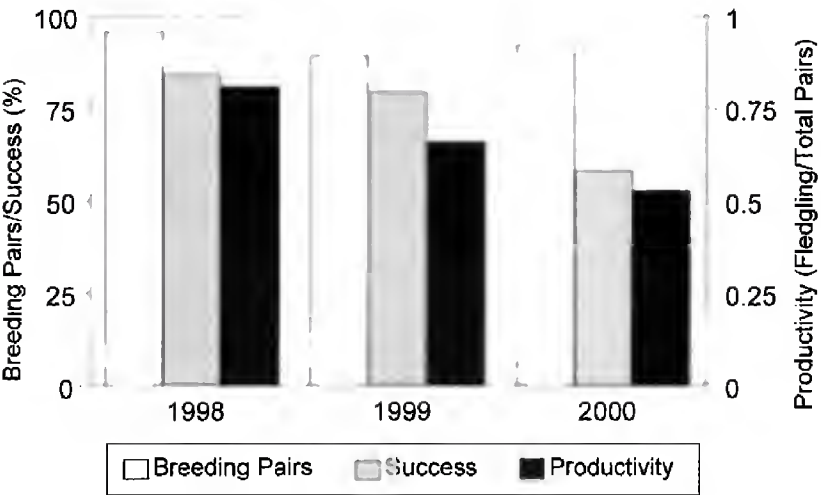


Figure 1. Reproductive performance of the Cinereous Vulture population at Sierra de San Pedro (Extremadura, Spain) in 1998–2000. Breeding pairs = percent of monitored pairs that laid a clutch; Success = percent of reproductive pairs (pairs that laid a clutch) that produced a young; Productivity = Number of fledglings produced per monitored pair.

The alkaline-phosphatase (ALP) concentration was measured in the plasma sample using a multiparametric autoanalyzer (Falcor 300, Menarini Diagnostics, Barcelona, Spain) with the reagents recommended by Menagent (Menarini Diagnostics). This variable was used as an index of chicks' condition at the moment of sampling, because it has been found to be positively associated with physical condition in the chicks of this species (Villegas et al. 2002).

The annual fledgling sex ratio is expressed as the proportion of males. The *G*-test was used to analyze deviations from the proportion 1:1, inter-yearly differences in this parameter, and in the productivity. Inter-year and gender variations in the chicks' physical condition were analyzed using a two-way analysis of variance in which sex and year were used as the principal factors and the alkaline-phosphatase concentration as the dependent variable (Zar 1999).

RESULTS

The percentage of Cinereous Vulture pairs initiating a clutch was similar in the 3 yr of study ($G = 0.52$, $df = 2$, $P = 0.77$). Productivity, however, declined from 0.81–0.53 during the study period (Fig. 1). There were statistically significant differences among years ($G = 28.9$, $df = 2$, $P < 0.01$), with the lowest value in 2000 (1998 vs. 2000: $G_{adj} = 27.6$, $df = 1$, $P < 0.01$; 1999 vs. 2000: $G_{adj} = 5.77$, $df = 1$, $P < 0.05$).

Of the 57 chicks monitored, 32 were males and 25 females, so that the overall fledgling sex ratio for the 3 yr was 56.1%. This was not significantly different from 50% (Table 1). By years, there was an increase in the proportion of males in 2000 (0.7), although the difference from the 1:1 proportion was not statistically significant in any year (Table 1). Likewise, there were no inter-year differences in the proportion of males ($G = 1.057$; $df = 2$, $P = 0.78$). The results were the same for the analysis of the 29 chicks of the selected family groups (Table 2).

The fledglings' physical condition, as measured by the ALP concentration (Table 3), differed among years ($F_{2,51} = 4.17$, $P = 0.02$), but not between sexes ($F_{1,51} = 1.01$, $P = 0.31$), and the interaction of these factors was not significant ($F_{2,51} = 0.73$, $P = 0.49$). In 2000, the chicks of both genders exhibited condition indices that were lower than in 1998 and 1999 (Table 3).

DISCUSSION

The inter-year differences found in the productivity reflect differences in the breeding conditions experienced by the individuals in the three seasons. At the time of breeding, the environmental, parental quality, or both were poorer in 2000, than in 1998 or 1999. The decline (Fig. 1) was mainly due to egg loss or the death of hatchlings, as the percentage of pairs that initiated a clutch was similar in each of the 3 yr. This decrease in productivity was accompanied by a significant decline in nutritional condition of the chicks at the time of sampling (Table 3). Costillo et al. (2002a) suggested adverse weather conditions as the cause of this decline in the area in the year 2000. Rain and cold at the time of hatching significantly affected the parents' capacity to provide food, thus could have led to a decrease in the hatchlings' physical condition, and even to their death from starvation (Donázar et al. 1988, Corbacho and Sánchez 2000, Dawson and Bortolotti 2000).

Various studies on raptors have found evidence for the parents being able to adjust the sex ratio of their progeny, or for the existence of a gender bias in early nestling mortality, according to each year's parental or ecological conditions (e.g., Olsen and Cockburn 1991, Wiebe and Bortolotti 1992, Dzus et al. 1996, Korpimäki et al. 2000, Arroyo 2002, Van den Burg et al. 2002). These studies

Table 1. Sex ratio variation at the fledging stage in Cinereous Vultures by year in Spain. Sex ratios are expressed as percentage of males.

YEAR	MALES	FEMALES	SEX RATIO	G-TEST	P-VALUE
1998	6	5	54.5	0.00	1.00
1999	13	13	50.0	0.00	1.00
2000	13	7	65.0	1.26	0.26
Pooled	32	25	56.1	0.63	0.43

Table 2. Sex-ratio variation at the fledging stage in Cinereous Vultures by year, within selected groups in Spain. Sex ratios are expressed as percentage of males.

YEAR	MALES	FEMALES	SEX RATIO	G-TEST	P-VALUE
1998	3	4	42.8	0.00	1.00
1999	7	5	58.3	0.08	0.77
2000	7	3	70.0	0.91	0.34
Pooled	17	12	58.6	0.55	0.46

used model species with marked sexual dimorphism and with brood sizes greater than one, in which gender-dependent food demand in combination with hatching asynchrony cause the cost-benefit ratio of rearing male and female chicks to differ (Dijkstra et al. 1998).

Most raptors exhibit reversed sexual size dimorphism, with the females being larger (Newton 1979). Growth demands, and hence the nutritional requirements, of female chicks are therefore greater, so that females are more costly for the parents to rear and they are more vulnerable to adverse environmental conditions (Richner 1991). Differences between species in the magnitude of their sexual dimorphism are often related to the agility of the prey, with greater dimorphism corresponding to greater agility (Newton 1979). In vultures, which feed on carrion, although the females are larger, the difference is slight, and there is a high degree of overlap in the sizes of the two sexes (Cramp and Simmons 1980, Donazar 1993). Studies of bird species that show little dimorphism have not shown any gender-environment interaction in chick performance (e.g., Sheldon et al. 1998, South and Wright 2002).

Differences in nutritional condition between males and females should most likely be observed when the environmental conditions were seriously limiting—a situation that did not arise in this area during the study period, as deduced from the high percentage of pairs that initiated a clutch and successfully reared a fledgling (Costillo et al. 2002a). Nonetheless, this does not imply that the costs associated with rearing the two genders are equal. In the case that the growth rate or the energy requirements of one sex are greater than those of the other, rearing a chick of the more costly gender in years

with suboptimal conditions, as year 2000 was, would involve greater effort for the parents. The result could be a greater decline in their physical condition over the course of the breeding season, which could compromise chick's survival and even the parents' capacity to breed in the following year (Donazar 1993, Korpimäki et al 2000, Genovart 2002). In such case, female Cinereous Vultures might obtain fitness benefits by producing a chick of the cheaper sex when the breeding conditions are not optimal (Meyers 1978), with the advantage that, by laying only a single egg, they can allow themselves to reabsorb a zygote of the unsuitable gender without incurring the costs of hatching asynchrony or of a significant lengthening of time on the clutch (Emlen 1997).

In summary, our results suggest a shift toward males of this Cinereous Vulture population's fledgling sex ratio in years with suboptimal breeding conditions (Table 1), although probably because of the small sample size, this bias was not statistically significant. This bias could reflect a greater production of males at hatching or a greater early mortality incidence of females.

RESUMEN.—Estudios empíricos recientes en rapaces han proporcionado evidencias de la existencia de sesgos significativos en la proporción de sexos de volantes en función de las condiciones ambientales experimentadas por los padres durante la estación reproductiva. La mayoría de estos estudios se han centrado en especies con un marcado dimorfismo sexual y con tamaños de nidada mayores que uno. En este trabajo estudiamos los patrones de variación en la proporción de sexos de volantes en una población de la Península Ibérica de *Aegypius monachus*, un ave rapaz con un dimorfismo sexual poco acu-

Table 3. Alkaline phosphatase concentration (UI/L) in male and female Cinereous Vultures during 3 yr in Spain.

YEAR	MALES		FEMALES		POOLED ^a		P ^b
	MEAN ± SD	(N)	MEAN ± SD	(N)	MEAN ± SD	(N)	
1998	1574.5 ± 232.9	(6)	1376.4 ± 186.4	(5)	1484.5 ± 227.4	(11) A	ns
1999	1437.1 ± 262.5	(13)	1343.0 ± 341.0	(13)	1390.0 ± 302.0	(26) A	ns
2000	1168.9 ± 284.9	(13)	1219.6 ± 249.9	(7)	1186.6 ± 267.6	(20) B	ns

^a The different letters in this column indicate that the differences between the year 2000 and the years 1998 and 1999 were significant
^b Probability that concentrations were different between males and females.

sado y con un tamaño de nidada igual a uno, durante el periodo 1998–2000. Analizamos si las variaciones anuales en el éxito reproductivo tienen alguna influencia en la proporción de sexos y en la condición nutricional de los pollos, medida por la concentración de fosfatasa alcalina en plasma, y si ésta muestra diferencias entre pollos de distinto sexo. Tanto la productividad de la población como la condición física de los pollos fue menor en el año 2000 que en los dos años previos. La proporción de sexos no se apartó de forma significativa de 1:1 ni mostró diferencias interanuales significativas, aunque la proporción de machos incrementó a 0.70 en el año de menor productividad. La condición nutricional no mostró diferencias significativas entre pollos de distinto sexo. Estudios más detallados son necesarios para determinar los mecanismos que actúan en la desviación de la proporción de sexos en esta especie.

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NEST PROVISIONING OF THE ORIENTAL HONEY-BUZZARD (*PERNIS PTILORHYNCHUS*) IN NORTHERN TAIWAN

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KEY WORDS: *Oriental Honey-buzzard*; *Pernis ptilorhynchus*; nest provisioning; paper wasps; *Polistes*; *Parapolybia*; Taiwan.

Raptors in the genus *Pernis* have a unique diet consisting primarily of the larvae, pupae, and adults of social Hymenoptera (Clark 1994, Orta 1994, Bijlsma 1999, Gamauf 1999). The European Honey-buzzard (*P. apivorus*) has been studied in some detail (Kostrzewa 1987a, 1987b, 1987c, Steiner 1992, Saporetti et al. 1994, Selas 1997, Van Manen 2000), but the biology of the Oriental Honey-buzzard (*P. ptilorhynchus*) has not been studied in depth (Clark 1994, Orta 1994, Morioka et al. 1995).

Based on our monthly raptor surveys in northern Taiwan's Yangmingshan National Park (25°10'N, 121°33'E) between 1993 and 2003, the Oriental Honey-buzzard was a common spring and autumn migrant, a rare winter visitor, and an uncommon summer resident. We found one Oriental Honey-buzzard nest in 1994 and one in 1999.

This paper reports the composition, seasonal variation, and relative importance of the prey species provisioned to the nest in 1999 and compares the male and female contributions to the nestling.

METHODS

We constructed a hide eye-level with the nest on a steep slope about 30 m away. We monitored the nest provisioning of the parents and recorded the time and the gender each time an adult returned to the nest. The male could be distinguished based on an orange-brown iris and broader dark tail bands, while the female has a yellow iris and narrower dark tail bands (Morioka et al. 1995). We simultaneously videotaped the nest-provisioning events. From these videotapes, we identified prey by comparing these with reference specimens in terms of structure, shape, color, and size of the wasp nests, the color and placement of the stem of the wasp nests, and

the color of the seal on cells containing pupae. Observations were made from 12 July–19 August, the day before the nestling fledged.

Because it was impossible to determine the exact sizes of the wasp nests from the videotapes due to filming angles, we collected empty wasp nests discarded under the honey-buzzard nest for species identification and counted the number of cells per wasp nest. Based on the sizes of these wasp nests, we categorized all the wasp nests in the videotapes into small, medium, or large classes (Table 1).

To understand the relationship between wasp activity and prey capture rate, we identified the paper wasps active in July and August. We searched for wasp nests along three trails in the study area through wooded areas with small cabins, each 1 km in length. We scanned the vegetation from canopy to the shrub layer and checked buildings carefully. Each transect line was searched at least twice to ensure the discovery of all wasp nests. For each wasp nest found, we measured height above ground, its length and width, recorded the number of cells, and described its shape. We collected one actively-used nest for each species found in order to obtain the proportion of cells occupied by eggs, different larval instars and pupae, and measured the mass of larvae at each instar.

Biomass per wasp nest was calculated with the following equation: Biomass = the number of cells/nest × proportion of cells occupied × the mean biomass/larva. The number of cells found on each wasp nest was related to size (Table 1). We used the wasp nests we collected as standards to determine cell occupancy and larval mass. Biomass estimates of reptiles and frogs were based on the mean mass of >10 individuals per species caught in the study area.

RESULTS

Food Composition and Seasonality. We observed the honey-buzzard nest for 26 d (204.7 hr) and recorded 123 food items delivered by parents. Among these, 78.9% were complete wasp nests ($N = 97$), 16.3% were Swinhoe's brown frogs (*Rana swinhoana*; $N = 20$), and 4.9%

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Table 1. Wasp nest-size classes and their cell numbers.

SPECIES	SIZE RANK	CELL NUMBER
<i>Polistis tenebriocosus</i>	Small	<39
	Medium	40–69
	Large	>70
<i>Polistis rothneyi</i>	Small	<119
	Medium	120–219
	Large	>220
<i>Polistis gigas</i>	Small	10–19
	Medium	20~29
	Large	>30
<i>Polistis</i> sp.	Medium	780
<i>Parapolybia varia</i>	Small	<179
	Medium	180–349
	Large	>350
Unidentified wasp comb (<i>Po. tenebriocosus</i> or <i>Po. rothneyi</i>)	Small	60
	Medium	80
	Large	100

were yellow-mouthed japalura lizards (*Japalura polygonata xanthostoma*; $N = 6$). All 97 wasp nests belonged to paper wasps (Polistinae, Vespidae), but two belonged to an unknown species and 24 could not be distinguished between *Po. tenebriocosus* and *Po. rothneyi* because either the nestling blocked the camera or the speed of delivery was too rapid. Among prey items that could be identified, *Po. tenebriocosus* nests ($N = 36$) constituted 29.3%, *Po. rothneyi* 13% ($N = 16$), *Po. gigas* 9.8% ($N = 12$), *Parapolybia varia* 5.7% ($N = 7$), and *Polistis* sp. 1.6% ($N = 2$). The frequency distribution of wasp nests brought back to the nestling was not different from those found along our transect lines (nests recorded: 29, *Po. tenebriocosus* = 21, *Po. rothneyi* = 3, *Po. gigas* = 2, and *Pa. varia* = 3, *Polistis* sp. = 0, $\chi^2 = 5.657$, $df = 4$, $P > 0.05$).

The body sizes of these five species of paper wasps varied from the world’s largest paper wasp (*Po. gigas*; 4.5 cm for adult males) to a new species, *Polistis* sp. (1.3 cm). The colony sizes of these wasps also varied from 12 cells in a *Po. gigas* nest to more than 400 cells in a *Pa. varia* nest. Based on biomass estimates from the nests we collected, we found that the pupae and the fourth and fifth instars of *Po. tenebriocosus*, *Po. rothneyi*, *Po. gigas*, and *Pa. varia* constituted 93.4%, 95.4%, 95.7%, and 87.6% of the total biomass of a nest, and occupied 44%, 45%, 56%, and 39.6% of the cells, respectively. We did not find any nests of the new *Polistis* sp. to obtain larva/pupa mass measurements. Because nests of this species were brought back only twice during the entire study period, we decided not to include this species in our biomass calculations.

Considering the cumulative biomass of all prey types delivered to the honey-buzzard nest, frogs and lizards together made up 16.9%, while Polistinae wasps made up

Table 2. Relative biomass of different prey types brought to the Oriental Honey-buzzard nest in northern Taiwan.

SPECIES	TOTAL	
	BIOMASS (g)	PERCENT
<i>Polistis tenebriocosus</i>	1003.00	31.59
<i>Po. rothneyi</i>	689.34	21.71
<i>Po. gigas</i>	244.50	7.70
<i>Parapolybia varia</i>	90.84	2.86
Unidentified nests ^a	611.16	19.25
Frogs	500.00	15.75
Lizards	36.00	1.13
Total	3174.84	100.00

^a Either *Po. tenebriocosus* or *Po. rothneyi*. We calculated the biomass by using the mean mass and mean cell occupancy of the two species.

83.1% (Table 2). Frogs were delivered in July and early August, and lizards were delivered in July only. By mid-August, honey-buzzards provisioned only paper wasps (Fig. 1). The patterns of seasonal variation were similar by prey frequency and by biomass. The biomass delivered to the nest per hour of observation fluctuated between 5–40 g throughout the nestling period except on the third d before fledging (Fig. 2). We did not monitor the nest on 18 August and so were unable to determine if this increased rate of prey delivery took place two consecutive days before fledging.

Paper Wasp Nest Height Distribution. The 29 paper wasps nests we found along trails hung from vegetation ($N = 10$) or eaves ($N = 19$) from 0.5–11.5 m above the ground. More than 86% were between 0.5–4 m high, the remaining four nests were above 6 m (3 *Po. tenebriocosus* and 1 *Po. rothneyi*).

Sexual Differences in Contribution. The male made

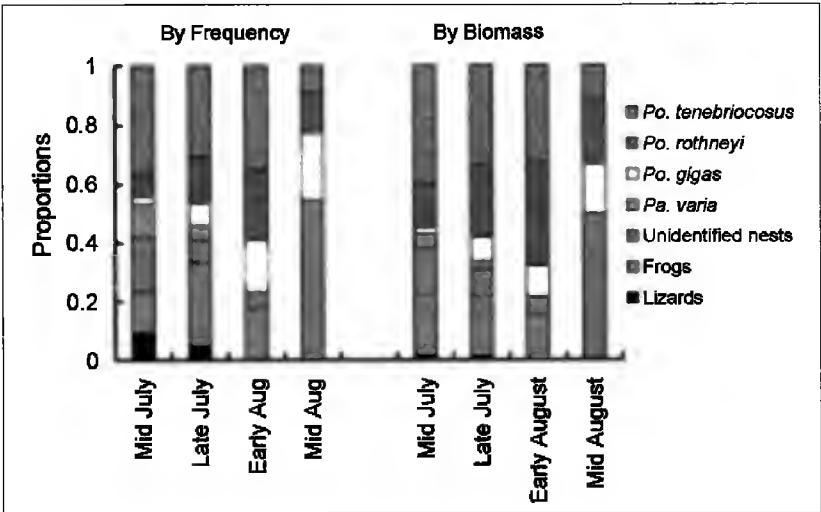


Figure 1. Diet of Oriental Honey-buzzard nestling based on the frequency of prey deliveries to the nest. Paper wasps in diet included: *Polistis tenebriocosus*, *Po. rothneyi*, *Po. gigas*, and *Parapolybia varia*.

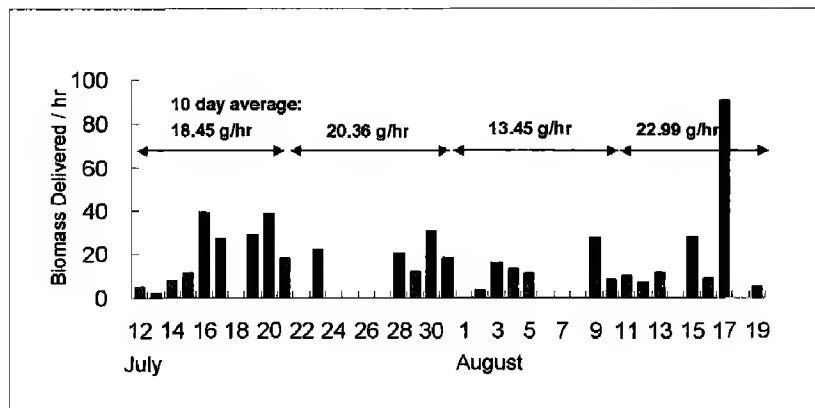


Figure 2. Biomass delivered to an Oriental Honey-buzzard nest in northern Taiwan per hour of observation. The nestling fledged on 20 August. The mean biomass delivered per hour for each 10-d period is given at the top of the histogram.

49.6% of the visits and the female 29.3%; the sex was uncertain in the remaining visits. Among the biomass delivered by adults of known sex, the male contributed 56% and the female 44% in July and in early August. After 9 August, female contribution ceased completely. The difference in biomass contribution between sexes across time periods was significant ($\chi^2 = 305.31$, $P < 0.0001$). Even if all the unknown feedings were made by the female, the male still would have contributed more biomass than the female during the final 10 d before fledging.

DISCUSSION

Prey Choice. Oriental Honey-buzzards captured prey that were on the ground, such as frogs in the shrub layer, or in the sub-canopy paper wasp nests. The pair we studied in Yangmingshan primarily brought *Polistes* nests as food for their young. Among known wasp prey, the frequency of different species of wasp nests they brought to the nestling was proportional to those available in the environment. However, they ignored the nests of the small paper wasp, *Po. takasagonus*, even though these nests were as common as the *Po. tenebriocosus* nests along our transect lines. A colony of *Po. takasagonus* was constructing a nest just below the honey-buzzard nest, but the honey-buzzards never showed interest in it. The biomass of the largest *Po. takasagonus* nest we found weighed less than 9 g, less than the smallest nest brought back by parents (9.91 g). There may be a minimum-size threshold for a wasp nest to be energetically profitable for honey-buzzards.

Another potential prey are *Vespa* hornets (Vespidae, Vespinae), which are large, conspicuous, and usually number by the hundreds per colony. The nests of some species are built on high branches and can be as large as 60 cm in diameter (M.C. Kuo pers. comm.). Hornets and wild bees (Apidae) were active within the home range of the honey-buzzard pair, but the nests of these families were never delivered to the nestling.

The honey-buzzards' food choice was most likely influ-

enced by the accessibility of prey and its energy content in relation to the handling cost. Hornets are aggressive and usually defend their combs vigorously (Evans and Eberhard 1970, Kuo and Yeh 1987). Ranking the aggressiveness of wasps into five classes (1 being most aggressive), *Po. tenebriocosus* and *Po. gigas* would be in class 5, *Po. rothneyi* and *Pa. varia* in class 3, while the *Vespa* species would be in classes 1–3 (Kuo and Yeh 1987). Although the stomach contents of European Honey-buzzards contained small numbers of hornets (Loskutova 1985), and adult Oriental Honey-buzzards probably consume hornets, preying on hornet nests no doubt demands a high energy cost. Specifically, honey-buzzards would need to evade the attack of a large number of hornets and would have a high risk of injury.

Wild bees are common in Taiwan, but most nest in rock crevices and tree cavities (Kuo and Yeh 1987). *Polistinae* nests in Taiwan always hang by a stem, which makes them easy for honey-buzzards to remove in flight. When paper wasps are abundant, there should be little incentive for a honey-buzzard to open logs or remove rocks to access a bee nest.

Seasonal Variation in Prey Composition. Paper wasps in Taiwan generally establish colonies in late April or May, and colony expansion usually occurs in June and July, followed by a mating period in July or August before they enter the dormant wintering stage, when breeding and foraging activities cease (Kuo and Yeh 1987, Lu et al. 1992). Based on this chronology, wasp nests would be small in the early part of the breeding season (July). During this period, the Oriental Honey-buzzards delivered wasp nests to the nestling and supplemented the nestling's diet with frogs and lizards. By mid-August, although frogs and lizards were still common, wasp colonies were large and the honey-buzzards delivered only paper wasp nests. European Honey-buzzards also foraged almost entirely on wasp nests when wasps were available (Martin 1992, Ferguson-Lee and Christie 2001).

European Honey-buzzards find wasp nests by watching the insects return from foraging trips (Grigor'yev et al. 1977, Martin 1992, Ferguson-Lee and Christie 2001). We do not know if Oriental Honey-buzzards could determine whether a wasp was departing from or returning to its nest. However, by following a flying wasp, honey-buzzards could either find the wasp foraging or come upon a nest.

Timing of Breeding. If the two nests we found are typical for this species, the Oriental Honey-buzzard has a much later breeding season than the other species of raptors in Taiwan. The hatching of eggs in July appears to be timed with the increase of paper wasp colonies in our study area. The delayed onset of its breeding season could result from the unavailability of wasp nests earlier in the spring. Wasp abundance has been known to influence the breeding success of European Honey-buzzards (Kostrzewa 1987c, Saporetto et al. 1994, Steiner 2000).

Sexual Differences in Provisioning. From mid-July to early August, the female Oriental Honey-buzzard contrib-

uted more than 30% of the biomass delivered to the nestling, and the male at least 40%. After 9 August, the female's contribution ceased completely even though she remained in the vicinity of the nest. Using a modeling analysis, Brodin et al. (2003) showed that whether a female raptor assisted with hunting for the young late in the nestling period depended on the hunting success of the male, environmental conditions, and the energy demands of the young. Because the pair of honey-buzzards we monitored had only one nestling, perhaps the male alone could provide sufficient prey for the young (reported clutch size for Oriental Honey-buzzard is two eggs; Sung et al. 1991).

Our study advanced what was known about Oriental Honey-buzzard. We found that adults primarily brought paper wasps as prey for their nestling, and the frequency of each species of wasp nest brought back reflected prey availability. Low energetic profitability most likely made some species of wasp nests undesirable. In addition, our results from one nest showed that the female delivered food less often and contributed less biomass to the nestling than the male.

RESUMEN.—Se conoce muy poco sobre la ecología y el comportamiento de *Pernis ptilorhyncus*. Con base en censos realizados entre 1993 y 2003, se determinó que esta especie es un visitante poco común durante el verano en Yangmingshan, Taipei, Taiwan. Encontramos un nido en 1994 y otro en 1999. A través de observaciones directas y de grabaciones de video realizadas en 1999, registramos las presas llevadas al nido durante 26 días, entre el 12 de julio y el 19 de agosto ($N = 204.7$ hr, $N = 123$ presas). Nuestros resultados revelaron que el 78.9% (83.7% en términos de biomasa) de los ítems alimenticios fueron nidos de avispas, el 16.2% (15.3% en biomasa) fueron ranas y el 4.9% (1.1% en biomasa) fueron lagartijas. Cinco especies de avispas que construyen nidos de papel fueron identificadas: *Polistes tenebriocosus*, *Po. rothneyi*, *Po. gigas*, *Parapolybia varia* y *Po. sp.* Las ranas y lagartijas fueron registradas sólo entre el 12 de julio y el 10 de agosto. La dieta de la cría de *P. ptilorhyncus* reflejó la fauna disponible de avispas y el ciclo anual de éstas en el área de estudio. Los machos y hembras no contribuyeron igualmente a alimentar a su cría. Las hembras dejaron de llevar alimento diez días antes de que el pichón abandonara el nido.

[Traducción del equipo editorial]

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WINTER DIET OF THE GREATER SPOTTED EAGLE (*AQUILA CLANGA*) IN THE AMVRAKIKOS WETLANDS, GREECE

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KEY WORDS: Greater Spotted Eagle, *Aquila clanga*; diet; winter; wetland; Amvrakikos, Greece.

The Greater Spotted Eagle (*Aquila clanga*) is a globally-threatened raptor, which breeds from Eastern Europe to the Pacific coast of the northern Far East and winters locally in southern Europe, Asia, the Middle East, and sub-Saharan Africa as far south as Uganda and Kenya (Tucker and Heath 1994). The main reasons for its decline are habitat destruction and degradation (in both forests, where the species nests, and wetlands, where it forages), disturbance during the breeding season, illegal shooting (mainly in migration), and to a lesser extent, nest robbing (Tucker and Heath 1994, Meyburg et al. 2001). The primary proposed conservation measures include the establishment of protected areas in the breeding habitat of the species, preservation of a mosaic of breeding-feeding habitat, protection of wetlands, avoidance of disturbance during the breeding season within 300 m of nests, as well as improvement of legislation,

international cooperation, monitoring, and research (Meyburg et al. 2001). The biology of the Greater Spotted Eagle has not been examined to a great extent; additionally, its diet has been examined almost exclusively during the breeding season (e.g., Priklonsky 1960, Galushin 1962, Pankin 1972, Ivanovsky 1996). Few studies of any kind have been conducted in the winter quarters of this species (Moltoni 1943, Francois 1992, Qingxia 1996).

Although an important population of Greater Spotted Eagles winters in the extensive wetlands of northern and central Greece (45–85 individuals), up to now it has received very little attention (Hallmann 1989, Handrinos and Akriotis 1997). Here, we present the results of an examination of Greater Spotted Eagles at a key wintering site, the Amvrakikos wetlands, western Greece, where up to 12 individuals winter each year.

STUDY AREA AND METHODS

Our study area was in the Amvrakikos wetlands, western Greece (38°59'–39°11'N, 20°44'–21°07'E). Amvrakikos is a Ramsar Wetland, a Special Protection Area, and proposed National Park. It is one of the largest wetlands in Greece covering 220 km² including river deltas, coastal

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lagoons, extensive saltmarshes, reedbeds, relic riparian woods, and grazed grasslands. Large areas bordering the salt marshes have been drained and support intensive agriculture and livestock farming. The roost site of the Greater Spotted Eagles observed was located in a small clump of very tall *Eucalyptus* trees on the banks of the Arachthos River, <2 km away from a major village. This roost is ca. 2 km from the estuarine wetlands of the river delta and is in a region of intensive agriculture, dominated by citrus plantations. The scattered trees along the bank of this region of the river include white poplar (*Populus alba*), willows (*Salix* sp.), ashes (*Fraxinus* sp.), and common alder (*Alnus glutinosa*). Amid the native riparian trees are a few planted eucalyptus (*Eucalyptus* sp.), some reaching a considerable height (ca. 40 m). In the winter of 2001–02, eagles roosted exclusively on the *Eucalyptus* sp., but they did not seem to use these trees in the winter of 2002–03, although they did gather to roost in the tree stands in the vicinity. In other parts of Amvrakikos, eagles roost on oaks (*Quercus* spp.) in the adjacent limestone hills (100–300 m elevation) 1–5 km away from the wetland habitats. We located four such roosts in the Amvrakikos, but pellets were collected only from the one at the Arachthos Delta because the others were in relatively inaccessible areas (steep, forested hills), or difficult to pin-point with precision (woodlots in marshes).

The diet of the species was studied by the analysis of pellets that were collected in January and March 2002 from under the regular roost, in a small *Eucalyptus* clump, which was used by six to seven Greater Spotted Eagles. Up to two Common Buzzards (*Buteo buteo*) were also seen to use the trees near the *Eucalyptus* trees, but not near the eagles. Buzzard pellets were easily distinguished from those of the eagles by a combination of both size and form (eagle pellets were ca. 70–120 × 30–50 mm and had a generally loose form, while those of buzzards were ca. 50–75 × 20–35 mm and were quite compact). Because of these differences and in combination with their location, we feel that it is unlikely that pellets of the two species were confused. Prey remains were identified with the help of reference books (Brown et al. 1987, Chinery 1993, Macdonald and Barrett 1993). The number of prey items was determined by counting the number of skull and major limb bones represented, when these were present; unless these indicated otherwise, we assumed the presence of one individual of each prey type per pellet.

RESULTS

We collected 57 pellets from the *Eucalyptus* roost, used by 6–7 individuals. The size of the pellets was ca. 70–120 × 30–50 mm. In the study area, the Greater Spotted Eagle preyed primarily on birds, but it also took mammals, reptiles, amphibians, fish, and insects (Table 1). By numbers, among 95 prey items, birds comprised 84.2% of the diet, followed by insects, mammals, reptiles, fish and amphibians (Table 1). By mass, birds were even more important (94.6%), while other prey were of comparatively minor importance. The most important birds, in terms of biomass, were ducks, particularly Eurasian Wigeons (*Anas penelope*) and Common Teals (*Anas crecca*), as well

as Common Moorhens (*Gallinula chloropus*), Common Coots (*Fulica atra*), Little Egrets (*Egretta garzetta*), and small gulls (*Larus* spp). We also found lead shot in 3.2% of the pellets.

DISCUSSION

Although the sample was comparatively small, some interesting conclusions may be drawn. The proportion of birds found in the diet was higher in the Amvrakikos wetlands than in any other study of the Greater Spotted Eagle. Priklnsky (1960), in the mouth of the Belaya River, Russia, based on pellet analysis (78 pellets and 274 prey items) reported the diet of the species, consisting of 69.0% mammals, 23.0% reptiles, 7.7% birds, and 0.3% fish (only vertebrates included). In addition, insects occurred in 29.4% of the pellets and carrion (primarily moose [*Alces alces*]) in at least 20.5% of the pellets. Study of the prey remains in the nests of the eagles also revealed a predominance of mammals and birds. Most mammals were small rodents, while most reptiles were snakes. Priklnsky (1960) summarized the results of several studies as follows: mammals 66.0–88.6%, birds 46.2–97.0%, insects 5.5–34.0%, and reptiles 0.0–12.3% (occurrence in pellets). Galushin (1962) in the valley of the Oka River during the period 1954–57, found the following yearly variation in diet: mammals 42.6–68.0%, birds 32.0–69.0%, fish 0.0–1.8%, and reptiles and amphibians each 0.0–0.6% (based on prey numbers). In Byelorussia, Ivanovsky (1996) found that 50 prey items (from remains) were 53.8% mammals, 21.1% amphibians, 17.4% birds, and 7.7% reptiles. Qingxia (1996) studied the diet of the eagles wintering in the Lishan Nature Reserve (China) and found the diet consisted of about equal numbers of mammals and birds ($N = 68$ prey items). The mammals consumed were mostly rodents, as well as some rabbits, collectively making up 52.1% of the diet by biomass. A variety of bird species were also eaten (47.9% of diet by biomass), including several gamebirds (Phasianidae).

Often, the study of pellets can result in biased estimates of diet composition; that is, this methodology can lead to the underestimate of certain prey types (particularly amphibians) and the overestimate in others. Vlachos and Papageorgiou (1996) found that a large proportion of the prey delivered in the nests of Lesser Spotted Eagles (*Aquila pomarina*), as recorded by direct observation, consisted of frogs, but these were only infrequently represented in the pellet analysis. Also many, or all, of the insects found in pellets in this and other studies, may have been ingested secondarily (i.e., consumed by the eagle prey).

Nearly all the prey species identified inhabited wetland habitats, particularly the salt marshes and coastal lagoons (Table 1). Surprisingly, few species of prey from the adjacent agricultural lands were taken (e.g., the small rodents and beetles).

The high proportion of water birds in our study was

Table 1. Diet of the Greater Spotted Eagle (*Aquila clanga*) in the Amvrakikos Wetland (*N* = 57 pellets).

COMMON NAME	SCIENTIFIC NAME	NUMBER	PERCENT NUMBER	PERCENT BIOMASS
Insects	Insecta	5	5.3	<0.1
Ground beetles	Carabidae	5	5.3	<0.1
Fish	Pisces	2	2.1	3.1
Mulletts	Mugilidae	2	2.1	3.1
Amphibians	Amphibia	1	1.1	0.1
Frogs	<i>Rana</i> sp.	1	1.1	0.1
Reptiles	Reptilia	3	3.2	0.5
Snakes	Colubridae	3	3.2	0.5
Birds	Aves	80	84.2	94.6
Little Egret	<i>Egretta garzetta</i>	3	3.2	4.7
Eurasian Wigeon	<i>Anas penelope</i>	11	11.6	27.4
Common Teal	<i>Anas crecca</i>	17	17.9	15.9
Unidentified ducks	<i>Anas</i> spp.	5	5.3	7.8
Spotted Crake	<i>Porzana porzana</i>	1	1.1	0.3
Water Rail	<i>Rallus aquaticus</i>	2	2.1	0.7
Common Moorhen	<i>Gallinula chloropus</i>	16	16.8	14.9
Common Coot	<i>Fulica atra</i>	4	4.2	8.7
Unidentified rails	Rallidae	1	1.1	0.3
Northern Lapwing	<i>Vanellus vanellus</i>	1	1.1	0.6
Common Redshank	<i>Tringa totanus</i>	1	1.1	0.4
Common Snipe	<i>Gallinago gallinago</i>	1	1.1	0.3
Unidentified scolopacids	Scolopacidac	1	1.1	0.3
Yellow-legged Gull	<i>Larus cachinnans</i>	1	1.1	3.7
Unidentified small gulls	<i>Larus</i> spp.	5	5.3	4.7
Hooded Crow	<i>Corvus corone</i>	1	1.1	1.6
Reed Bunting	<i>Emberiza schoeniclus</i>	3	3.2	0.3
Unidentified passerines	Passeriformes	4	4.2	0.4
Unidentified birds	Aves	4	4.2	1.9
Mammals	Mammalia	4	4.2	1.7
Eastern Hedgehog	<i>Erinaceus concolor</i>	1	1.1	1.6
Unidentified voles	<i>Microtus</i> sp.	1	1.1	0.1
Unidentified mice	<i>Mus</i> spp.	2	2.1	0.1
Total	—	95	—	—

probably due to their high availability in the area, compared with other potential prey during the study period. The winter of 2001–02 was relatively “severe” with periods of frosts, thus reptiles and amphibians would hardly have been available to the eagles (in fact, the presence of reptiles and amphibians, even in low numbers, was surprising). This may be true, to a lesser extent, for the smaller mammals as well. On the other hand, large numbers of waterfowl winter in the Amvrakikos wetlands, including up to 100 000 ducks and coots in certain years. The eagles mostly hunt prey from perches (often on low tamarisk, *Tamarix* spp.), or from embankments, or patrolling by gliding low over extensive wetland areas,

where many water birds are present. These areas, as well as providing relatively abundant prey, also provide cover suitable for the eagles to surprise their prey. We made relatively few observations of the eagles over large open lagoons or the surrounding sandy spits, in which the highest numbers of waterfowl winter. As well as capturing healthy prey, the eagles probably also took injured or dead birds, as suggested by the presence of lead shot in two pellets. The presence of lead shot in the pellets indicated that the Greater Spotted Eagle fed on birds shot, but not retrieved by hunters (see also Hallmann 1989). Lead shot is considered to be a serious threat for many wetland raptors, such as the West-

ern Marsh-Harrier (*Circus aeruginosus*) in France (Pain et al 1997). Therefore, the potential effect of lead shot on the Greater Spotted Eagle should be investigated.

Stands of trees, which provide perches for look-outs and roosting, are important for the hunting eagles and should be protected. Riparian woodlots and large trees are often cut by local inhabitants, and thus roost sites (actual or potential) may be threatened by this activity.

Poisoning is also a potential threat. Because several unauthorized refuge dumps exist in the Amvrakikos Wetlands, the threat of poisoning through scavenging at dumps is present. Also, eagles could feed on poisoned carrion laid out illegally by local farmers for deterring foxes and other canines. Therefore, extent of scavenging and the susceptibility of the Greater Spotted Eagle to such poisoning should be investigated.

RESUMEN.—Se examinó la dieta de águilas *Aquila clanga* en los humedales de Amvrakikos en el oeste de Grecia por medio de análisis de egagrópilas. Con base en el número de presas, la dieta estuvo compuesta principalmente por aves (84.2%) y por cantidades menores de insectos (5.3%), mamíferos (4.2%), reptiles (3.2%), peces (2.1%) y anfibios (1.1%). Las aves fueron supremamente importantes en términos de biomasa (94.6%); las presas principales fueron patos del género *Anas*, y los rálidos *Gallinula chloropus* y *Fulica atra*. La gran mayoría de las presas correspondió a especies que se encuentran casi exclusivamente en humedales.

[Traducción del equipo editorial]

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GENDER DETERMINATION OF EURASIAN EAGLE-OWLS (*BUBO BUBO*) BY MORPHOLOGYMARIA DEL MAR DELGADO¹ AND VINCENZO PENTERIANI*Department of Applied Biology, Estación Biológica de Doñana (EBD), C.S.I.C., Avda. De María Luisa s/n. Pabellón del Perú, Apdo. 1056, 41013 Sevilla, Spain***KEY WORDS:** *Eurasian Eagle-Owl*; *Bubo bubo*; *discriminant function analysis*; *forearm*; *sexing*; *gender determination*.

Gender determination is an important prerequisite to studies on many aspects of avian biology such as foraging ecology (e.g., Anderson and Norberg 1981), evolutionary ecology (e.g., Clutton-Brock 1986), survivorship (e.g., Newton et al. 1983), and conservation genetics (e.g., Griffith and Tiwari 1995). Many avian species show no sexual dimorphism in plumage, but the gender of individuals may be determined by body measurements. Most raptors are dimorphic in size, which allows for the development of gender determination methods based on morphometric data. Nonetheless, this method has been applied to a relatively small number of species (e.g., Bortolotti 1984a, 1984b, Garcelon et al. 1985, Edwards and Kochert 1987, Ferrer and De Le Court 1992, Balbontín et al. 2001).

The Eurasian Eagle-Owl (*Bubo bubo*) is a sexually monomorphic species and, although females are bigger than males (i.e., reversed sexual dimorphism) gender determination in the field is only possible through detection of gender-specific calls (Penteriani 1996). Due to its conservation concerns, the high density of this species in several Mediterranean areas of its breeding range (e.g., Penteriani et al. 2002, Delgado et al. 2003, Penteriani et al. 2004), its eclectism in habitat preferences (e.g., Penteriani et al. 2001, Marchesi et al. 2002, Martínez et al. 2003), its complex social communication (e.g., Penteriani 2002, Penteriani 2003), and its impact on bird communities (e.g., Sergio et al. 2003), this species has been the subject of increasing research in the last few years. In this context, determination of gender for this species represents a useful tool in future studies examining intersexual and intrasexual patterns. Our objective was to provide an inexpensive and practical tool to determine the gender of eagle-owls in the field using a minimum number of morphometric measurements.

METHODS

We measured 13 morphological characteristics of 50 skins of Eurasian Eagle-Owls ($N = 22$ males and $N = 28$ females) from the collections of the Estación Biológica de Doñana (Andalusia, Spain) and the Natural Science

Museum of Madrid. All eagle-owls analyzed came from Spain and gender was previously determined by internal examination of reproductive organs. To avoid the confounding effect of age, we only used skins of adult individuals when morphometric differences seem to be mostly related to gender rather than age.

Length of claws, tarsus, bill including cere, exposed culmen without cere, and bill depth were taken using a caliper (± 0.1 mm) (Bortolotti 1984a, 1984c). The four claws of the left foot were measured from the hallux claw (toe number one) to the outer claw (toe number four). Length of wing chord, tail, ear tufts, and forearm (the length from the front of the folded wrist to the proximal extremity of the ulna) were measured with a metal ruler to the nearest mm (Bortolotti 1984a, 1984c). To minimize measurement errors, each specimen was measured three times. For analyses, we used the mean values of these three measurements.

To determine which morphometric variables were the best predictors for gender determination, we conducted a two-step analysis. First, a t -test was conducted for the 13 variables to identify the descriptors for which the between gender variance was higher. Secondly, we used a discriminant function analysis (DFA) to obtain the function best discriminating between males and females. Chi-square analysis was employed to test the significance of the gender classification established by the DFA procedure (Sokal and Rohlf 1995). DFA has been widely used for gender determination in bird species with monomorphic plumage (e.g., Sclaro et al. 1983, Maran and Myers 1984, Hanners and Patton 1985, Malacalaza and Hall 1988). A DFA produced a linear combination of several morphometric variables that best discriminated samples of individuals of known gender. This function was then used to predict the sex of unknown birds (Sokal and Rohlf 1981, Norusis 1988). Because large discriminant functions can be cumbersome (McCloskey and Thompson 2000), we established a level of significance of $P < 0.0001$ as a threshold to select the significant t -test variables that were used in the DFA.

RESULTS AND DISCUSSION

The t -test revealed that females were significantly larger than males in all the variables measured except tail, wing chord, and ear tufts (Table 1). Second claw, forearm, length of exposed culmen without cere, and bill depth were the most dimorphic variables ($P < 0.0001$). The DFA produced the following discriminant equation:

$$D = -28.740 + 0.204(\text{second claw}) + 0.714(\text{forearm}) + 0.158(\text{culmen without cere}) + 0.113(\text{bill depth}).$$

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Table 1. Morphometric of study skins of males and female Eurasian Eagle-Owls (*Bubo bubo*) from Spain. Claws are numbered according to toe numbers (hallux = 1, outer claw = 4).

	FEMALES (N = 28)			MALES (N = 22)			t	df	P
	\bar{x}	SD	RANGE	\bar{x}	SD	RANGE			
Claw of toe 1	34.62	3.56	26.74–40.10	30.60	3.33	21.66–33.98	−3.512	37	0.0010
Claw of toe 2	34.89	2.36	27.72–38.50	31.34	2.19	27.87–38.84	−5.252	44	0.0001
Claw of toe 3	30.53	3.12	25.32–36.84	28.35	2.42	24.99–33.67	−2.436	39	0.0201
Claw of toe 4	29.70	3.39	20.09–33.62	26.61	1.30	24.22–28.86	−3.806	38	0.0001
Tarsus (L)	102.5	6.58	83.98–112.00	93.8	4.5	80–104.00	−4.543	47	0.0001
Tail	258.76	14.73	229.67–293.67	250.36	15.70	232.33–293.00	−1.919	47	0.0613
Wing ^a	44.13	3.07	32.26–47.46	43.19	1.87	40.67–48.90	−1.260	47	0.2140
Forearm	20.04	0.84	18–21.93	18.83	0.72	17.06–19.76	−5.288	46	0.0001
BCER ^b	48.56	2.87	42.60–54.35	44.87	3.15	38.90–52.03	−4.280	47	0.0001
BCUL ^c	32.89	1.82	27.25–35.17	30.10	1.61	27.18–34.90	−5.523	46	0.0001
Bill depth	28.47	3.19	20.25–33.97	24.81	3.61	12.22–30.09	−3.750	47	0.0001
Ear tuft (left)	72.96	6.70	46–84	72.23	4.53	63.33–81.33	−0.421	44	0.6762
Ear tuft (right)	72.16	10.51	42.33–86.67	74.75	3.82	65–79.67	1.096	45	0.2790

^a Wing chord.
^b Bill including cere.
^c Exposed culmen without cere.

A correct classification was obtained for 90.5% of males and 90.9% of females. Hence, overall 90.7% of cases were classified correctly. This classification was significantly better than random (chi-square = 41.360, $P = 0.0001$). There was a clear separation between males and females along the first discriminant axis (Fig. 1).

Variables used in this study were easy to measure in the field and have been shown to be good predictors of gender in several other bird species (e.g., Calvo and Bolton 1997, Renner and Davis 1999, Leader 2000). Also, in comparison with other proposed morphometric criteria for gender determination (e.g., wing and body mass), the descriptors we used were not influenced by molting, condition of specimens, or of the feathers.

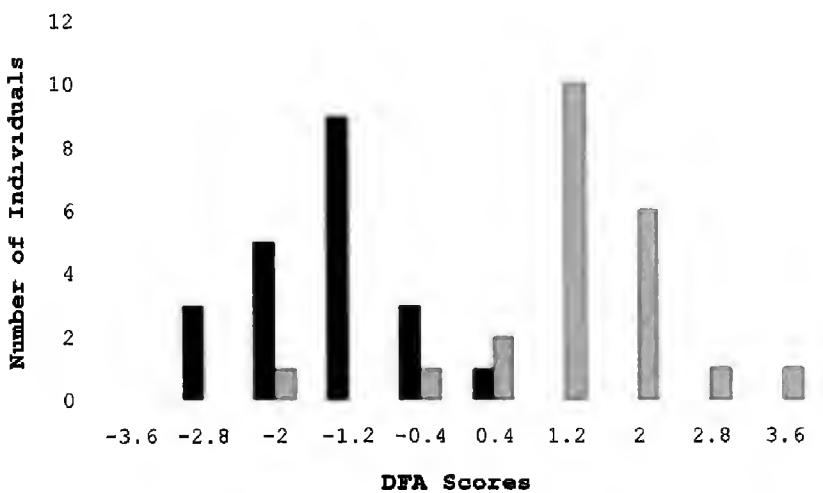


Figure 1. Discriminant Function Analysis (DFA) scores of male ($N = 22$) and female ($N = 28$) Eurasian Eagle-Owl study skins. The four variables used in classifying genders were: second claw, forearm, length of exposed culmen without cere, and bill depth.

The length of the forearm has been used successfully for gender determination in two other raptor species, Spanish Imperial Eagles (*Aquila adalberti*; Ferrer and De Le Court 1992) and Bonelli's Eagles (*Hieraaetus fasciatus*; Balbontín et al. 2001). In a similar study, Martínez et al. (2002) also considered this parameter to be the best predictor of gender for Eurasian Eagle-Owls. Additionally, our study revealed a small overlap between males and females. Finally, the forearm variable has two additional advantages: it is easy to measure, and repeated measurements taken by both the same and different observers show little variation (Ferrer and De Le Court 1992).

Gender determination by DFA is applicable to adults year round, when most alternative methods are limited by season (e.g., during the breeding season) or expensive (e.g., karyotyping). However, the application of our DFA model may be limited because of the pronounced geographical variation of body size exhibited by eagle-owls (Penteriani 1996). This factor needs to be taken into account when applying our DFA model to other populations. However, our approach could be used to derive similar DFA models for other Eurasian Eagle-Owl populations.

RESUMEN.—*Bubo bubo* es un ave rapaz nocturna grande que presenta dimorfismo sexual de tamaño revertido. A través del análisis de 13 parámetros morfológicos colectados de 50 especímenes de museo ($N = 22$ machos y $N = 28$ hembras), asignamos correctamente el género a 90.7% de los individuos por medio de análisis de función discriminante. Las variables morfológicas usadas para predecir el género incluyeron la profundidad del pico,

longitud de la segunda garra, longitud del antebrazo y longitud de la parte expuesta del culmen sin cera.

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LETTERS

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A POSSIBLE CASE OF DOUBLE BROODING OF EAGLE-OWLS (*BUBO BUBO*) IN SPAIN

Multiple breeding in the same reproductive season is a common life-history tactic by which individuals can increase their genetic representation in future generations (Roff 2002, *Life history evolution*. Sinauer, Sunderland, U.K.). However, this strategy implies costs in terms of survival, future fledgling production, or both, although such costs of reproduction depend closely on environmental conditions (Verhulst 1998, *Funct. Ecol.* 12:132–140). Perrins (1970, *Ibis* 112:242–255) hypothesized that females should start laying as soon as they are physiologically capable, and that interindividual differences in the timing of breeding could be caused by differential acquisition of food (food supply hypothesis). Early laying pairs are expected to be more able to carry out second clutches than pairs that lay later, because females are in a better physiological condition and they have time enough for additional breeding attempts in the same reproductive season (e.g., Morrison 1998, *Auk* 115:979–987; Marks and Perkins 1999, *Wilson Bull.* 111:273–276). Laying second and even third clutches has been reported as usual in a wide variety of bird species, mainly passerines (e.g., Friesen et al. 2000, *Wilson Bull.* 112:505–509; Mahony et al. 2001, *Wilson Bull.* 113:441–444), while it is considered as exceptional in others (e.g., Miller 2003, *Wilson Bull.* 115:94–95). In raptors, there are reports of double clutches (Newton 1979, *Population ecology of raptors*. T. & A.D. Poyser, London, U.K.), although most of them correspond to small-sized species with short reproductive periods and in favorable areas or years of high food availability (e.g., Korpimäki 1988a, *J. Anim. Ecol.* 57:1027–1039; Marks and Perkins 1999). For large species with long reproductive periods, even replacement clutches are rarely reported (Newton 1979, Bull and Henjum 1990, *Ecology of the Great Gray Owl*. USDA For. Serv. Gen. Tech. Rept. PNW-GTR-265, Portland, OR U.S.A.; Cabeza and de la Cruz 2001, *Ardeola* 48:233–236; Margalida and Bertran 2002, *J. Raptor Res.* 36:154–155; Martínez and Blanco 2002, *Ardeola* 49:297–299). Owls of the family Strigidae typically raise no more than one brood per year, but some records of double brooding have been reported (Kellomäki et al. 1977, *Ornis Fenn.* 54:124–135; Millsap and Bera 1990, *Wilson Bull.* 102:313–317; Forsman et al. 1997, *Condor* 97:1078–1080; Marks and Perkins 1999). Replacement clutches are known for Eurasian Eagle-Owls (*Bubo bubo*) (e.g., Blondel and Badan 1976, *Nos Oiseaux* 33:189–219), but only one possible double clutch has been reported in southeastern Spain (Martínez et al. 2003, *Ardeola* 50:77–79).

Collaborators and I have monitored a Eurasian Eagle-Owl population since 1999 in the province of Toledo, central Spain (39°47'N, 4°04'W). The study area extends over 2400 km² with meso-mediterranean climate, with mean temperatures of 26°C and 5°C in July and January, respectively, and 300–400 mm of rainfall concentrated in spring and autumn. To date, we have located 100 pairs of eagle-owls, but we estimated that at least twice this number could be breeding in the study area. Mean nearest neighbor distance (hereafter NND; \bar{x} = 1.4, SD = 1.7 km, N = 100) is the lowest, whereas clutch size (\bar{x} = 3.67, SD = 0.53, N = 36) and mean number of fledglings per successful pair (\bar{x} = 2.72, SD = 0.78, N = 50; J. Ortego unpubl. data) is the highest reported to date (Marchesi et al. 2002, *Ibis* 144:164–177). These population traits are likely related to the fact that rabbit (*Oryctolagus cuniculus*) density in the study area is one of the largest reported for the Iberian Peninsula (Blanco 1998, *Mamíferos de España*. Geoplaneta, Barcelona, Spain).

On 13 April 2002, I found three fledged chicks, which flew away when we approached them, around the nest of an eagle-owl pair. Approximately 50 m away from this nest, and in the same cliff, I found an adult bird incubating two eggs. In spite of the high density of eagle-owls in the study area, it seems unlikely that the second clutch belonged to a different pair. Eagle-owls are closely linked to ravines in the study area, which provide both nest sites with low human disturbance and high rabbit availability (Ortego and Díaz in press, *Selección del hábitat de nidificación del búho real [*Bubo bubo hispanus*] en la provincia de Toledo*. In *Actas de las XVI jornadas ornitológicas españolas*. Sociedad Española de Ornitología, Madrid, Spain). The minimum NND recorded in the study area was 150 m, and the minimum mean for pairs living in the same ravine was 389 m (N = 14 pairs). The NND for the pairs settled in the ravine where the reported nest was located was 895 m (N = 11). This relatively low density makes the settlement of two pairs in the same cliff unlikely.

According to chick development, I estimated the laying date for the three fledglings around 5 January. Laying date of this pair in the following breeding season was estimated around 19 December, the earliest for a sample of 31 pairs (\bar{x} = 28 January, SD = 17.5). The early laying date of this pair could have facilitated a second clutch (Morrison 1998; Marks and Perkins 1999; however, see Martínez et al. 2003). In addition, in the previous breeding season I found 17

young rabbits in this nest when the last egg was still hatching. Storage of rabbits in the nest before hatching is common in our study area (J. Ortego unpubl. data), and I have never noticed such a large number of rabbits in a sample of 36 nests. These data suggest that the pair involved could be living in a high quality territory that yields relatively large numbers of available prey of high-energetic value, consequently minimizing the costs of a multiple brooding (Verhulst 1998, *Funct. Ecol.* 12:132–140).

Martínez et al. (2003) offered two alternative explanations that could explain the apparent double-brooding observations in southwestern Spain. Death of the female could have allowed the male to pair with another female physiologically ready to start the reproduction, or the male could have been polygynous (Bull and Henjum 1990), as has been observed in other raptors responding to a superabundant food supply (Korpimäki 1988b, *Oecologia* 77: 278–285; Marti 1992, *Condor* 92:261–263). The latter explanation, polygyny, would be an usual breeding behavior in the eagle-owl (Dalbeck et al. 1998, *Vögelwelt* 119:331–344). Neither the pair reported by Martínez et al. (2003), nor the pair reported here were marked, so it was not possible to conclude if a lone pair was involved, or if a replacement, or if two females were involved in these cases of double-brooding. Nevertheless, all proposed explanations are likely related to the effects of high prey availability on the reproductive behavior of eagle-owls, which can reduce reproductive costs and lead to multiple breeding attempts. Such conditions in Spain seem to be infrequent, especially after the recent population crash of rabbits (Villafuerte et al. 1995, *Mammalia* 59:651–659; Martínez and Calvo 2001, *J. Raptor Res.* 35:259–262; Martínez and Zuberogoitia 2001, *J. Ornithol.* 142:204–211). However, intensive research in high-prey situations, such as reported here may provide further examples of double brooding that could be more common than previously thought (Marks and Perkins 1999; Mahony et al. 2001).

Consejería de Agricultura y Medio Ambiente de Castilla-La Mancha provided the permits for monitoring eagle-owl nests. I wish to thank Mario Díaz for idiomatic and editorial advice and José Arcadio Calvo for helping during field work.—**Joaquín Ortego (e-mail address: joaquinortego10@latinmail.com), Departamento de Ciencias Ambientales, Facultad de Ciencias del Medio Ambiente, Universidad de Castilla-La Mancha, Avda, Carlos III s/n, 45071 Toledo, Spain.**

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INSECT HAWKING OBSERVED IN THE LONG-EARED OWL (*ASIO OTUS*)

The Long-eared Owl (*Asio otus*) has been described as a specialist on a relatively narrow range of species of small mammals (Errington 1932, *Condor* 34:176–186; Craighead and Craighead 1979, Hawks, owls, and wildlife. Stackpole Co., Harrisburg, PA U.S.A; Marks and Marks 1981, *Murrelet* 62:80–82), and highly dependent on *Microtus* spp. in many parts of North America and Europe (Marks 1984, *Can. J. Zool.* 62:1528–1533; Marks and Marti 1984, *Ornis Scand.* 15:135–143). *Asio otus* has also been found to shift dietary preference seasonally among different *Microtus* spp. in southern Sweden and among other small mammals in central Slovenia (Nilsson 1981, *Ornis Scand.* 12:216–223, Tome 2003, *Ornis Fenn.* 80:63–70).

Invertebrates are a minor component of this species' diet (0.5–0.2% by number, <0.1% by mass; Marti 1974, *Condor* 76:45–61; Marti 1976, *Condor* 78:331–336; Tome 1994, *J. Raptor Res.* 28:253–258; Alivizatos and Goutner 1999, *J. Raptor Res.* 33:160–163) as are larger prey, such as juvenile (100–150 g) lagomorphs (0.75% by number, 2.5% by biomass, Marks 1984).

Foraging behavior among Long-eared Owls is less understood than diet. The long-pointed wings and relatively low-wing loading of Long-eared Owls suggests the ability to hunt aerially, which has been observed in the form of quartering the ground for prey. Such adaptations are similar to Caprimulgids such as the Common Nighthawk (*Chordeiles minor*) which “hawk” prey aerially (catching prey on the wing; Poulin et al. 1996, Common Nighthawk (*Chordeiles minor*), In A. Poole and F. Gill [Eds.], The birds of North America, No. 213. The Birds of North America, Inc., Philadelphia, PA U.S.A.). In the Long-eared Owl, hawking behavior has never been documented (Marks et al. 1994, Long-eared Owl (*Asio otus*), In A. Poole and F. Gill [Eds.], The birds of North America, No. 133. The Birds of North America, Inc., Philadelphia, PA U.S.A.). There are very few published observations of Long-eared Owl foraging

behavior, as this species is strictly nocturnal and difficult to observe. Glue and Hammond (1974, *Br. Birds* 67:361–369) report Long-eared Owls “hovering” seconds before making a kill of a small mammal, but not otherwise. During nocturnal owl and bat surveys, we were frequently able to observe the behavior of several owl species. Here, we report observations of a hovering/hawking approach to aerial feeding by a Long-eared Owl, not previously reported in this species.

Observations took place in the boreal forest of northern Ontario, Canada, south of the municipality of Ear Falls. The topography of the area is highly variable, with many lakes, and is dominated by stands of black spruce (*Picea mariana*) and to a lesser extent jack pine (*Pinus banksiana*).

On 25 June 2001, between 2220–2240 H, we first observed a Long-eared Owl perched on an aspen tree (*Populus tremuloides*) on the roadside. We confirmed the owl’s identification with a flashlight and a pair of binoculars. We were able to approach the bird three times to within 10 m as it perched on various trees. As we tried to find the bird a fourth time, it flew out from the side of the road and began to hover, slowly sweeping back and forth across the road ca 2 m off the ground within 5 m of our vehicle. In the headlights, we were able to observe the owl as it “hawked” moths over a large water puddle in the middle of the road. The moths were large enough to be clearly visible (ca 5.7–6.3 cm wingspan), and were later confirmed to be moths of the genus *Actius* or *Smerinthus* (Ross 1873, *The butterflies and moths of Canada*. Rowsell and Hutchison, Toronto, Canada), which had previously been observed in the area. While we watched, the owl captured at least three moths, which were apparently consumed whole. The owl then flew back into the woods in the direction from which it came, and was not seen again that night.

Comments on this observation from M.C. Drever and T.D. Nudds were greatly appreciated. We wish to thank the Sustainable Forest Management Network of Centres of Excellence and The University of Guelph for funding, and for cooperation from Weyerhaeuser Inc., all of whom contributed to our presence in the field during the summer of 2001.—**Darren J.H. Sleep** (e-mail address: dsleep@uoguelph.ca) and **Rowan D.H. Barrett**, Department of Organismal Biology, Ecology and Evolution, University of Guelph, Guelph, Ontario N1G 2W1, Canada.

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OSPREY SCAVENGES COMMON MURRE CARCASS IN COASTAL WASHINGTON

Ospreys (*Pandion haliaetus*) feed almost exclusively on fish (Poole et al. 2002, *In* A. Poole and F. Gill [Eds.], *The birds of North America*, No. 683. The Birds of North America, Inc., Philadelphia, PA U.S.A.). They rarely capture non-fish items or scavenge non-fish carcasses. Poole et al. (2002) provided no records of Ospreys scavenging bird carcasses.

On 9 September 2002, I observed an Osprey in immature plumage scavenging a Common Murre (*Uria aalge*) carcass on northern Grayland Beach, Grays Harbor County, WA. The carcass was one of >15 on the beach during my visit. Grayland Beach is a relatively flat, sandy beach situated between the mouths of Grays Harbor and Willapa Bay on Washington’s outer coast. At 1304 H, I saw an Osprey on the beach; it faced south and used its bill to twice tear at the flesh of a carcass that I later identified as a Common Murre. The Osprey then turned, apparently saw me (ca. 100 m away), and flew south and out of view. I approached the carcass, which lay on its back, and noted the pectoralis muscles were exposed and had been partially removed. I did not see the Osprey again, but at 1314 H saw another Osprey fly over heading south above the beach.

It is possible that the Osprey I observed was merely investigating an unusual item, a behavior that has been noted in post-fledging juveniles (L. Gilson pers. comm.), and that scavenging was not its initial intent. However, it seems reasonable that most scavenging is preceded by investigation, particularly in juveniles. Consequently, regardless of the original intent, the outcome was that the Osprey extracted flesh from the carcass of a dead bird.

Although Ospreys rarely capture or consume non-fish prey, Wiley and Lohrer (1973, *Wilson Bull.* 85:468–470) identified a number of factors to explain the occasional use of non-fish food. Among these factors were: (1) the presence of easily-captured prey and (2) an abundant alternate food source. The coastal beaches of Washington often have abundant dead birds (e.g., Northern Fulmar [*Fulmarus glacialis*], scoters [*Melanitta* spp.], gulls [*Larus*

spp.], and Common Murres) that wash ashore and are deposited at or above the high-tide line. These carcasses are occasionally scavenged by Peregrine Falcons (*Falco peregrinus*; Buchanan 1991, *Northwest. Nat.* 72:28–29), Bald Eagles (*Haliaeetus leucocephalus*), and Northern Harriers (*Circus cyaneus*; J. Buchanan unpubl. data). The presence of numerous carcasses on the beach during my visit represented an easily accessible and abundant source of food, two of the conditions proposed to explain use of non-fish food by Ospreys (Wiley and Lohrer 1973). Ospreys that use coastal habitats, especially during migration, have access to an easily obtained food source in some areas. I suggest that scavenging, although apparently rare, may be more likely in this coastal habitat than in other areas.

I thank Tracy Fleming for providing literature citations. Lauren Gilson, Jim Belthoff, and an anonymous reviewer provided comments that improved the manuscript.—**Joseph B. Buchanan** (e-mail address: buchajbb@dfw.wa.gov), Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501 U.S.A.

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HOW LONG IS TOO LONG? A CASE OF FOSTERING NESTLING BONELLI'S EAGLES (*HIERAAETUS FASCIATUS*)

After monitoring eight nests of Bonelli's Eagle (*Hieraaetus fasciatus*) for more than 11 yr in the state of Maharashtra, India, we recorded two incidents wherein eaglets were either found to have fallen out of nests due to human disturbance or removed by local children. In the two incidents, we replaced the previously-removed eaglets into the nest immediately upon discovery and then verified continued parental care.

To help ensure the continued survival of raptors in the wild, a wide range of techniques have been developed and applied to maximize the survival of the brood (see Cade et al. 1988, Peregrine Falcon populations: their management and recovery. The Peregrine Fund, Boise, ID U.S.A.) including “add-on” techniques (an abandoned nestling is introduced into a wild brood of similar age); guarding of nests during the breeding season; relocation of nests away from sources of mortality; presentation of alternative, artificial nest platforms or sites; translocation; hacking in natural or artificial nests; and inter- or intra-specific fostering by parents with young of the same age (Allen 1982, Pages 5–19 in T.N. Ingram [Ed.], Proceedings of the Bald Eagle conference on Bald Eagle restoration. USDI Fish and Wildlife Service, Rochester, NY U.S.A.). All of these techniques are very costly, do not always ensure success, and many are employed in human-modified environments. Here, we present a method that has not been previously employed in a natural environment with Bonelli's Eagles, though similar experiments have been conducted for the Spanish Imperial Eagle (*Aquila adalberti*; Gonzalez et al. 1986, *J. Raptor Res.* 20:77–78; Ferrer 1993, *J. Ornithol.* 134:335–337).

Our experiment was conducted unintentionally on 14 March 2003 when we discovered that local children had removed an eaglet from a Bonelli's Eagle nest in Jejuri, Pune district (18°31'N, 73°55'E), India. The eaglet was 40–42 d old and it was returned to the nest. We noted that there were no green branches on the nest, which was unusual because in previous seasons parents were observed to layer the nest with new leaves and branches almost on a daily basis. Moreover, the parents continuously evicted the eaglet over the next 3 d by pushing it out of the nest with their wings. Therefore, we decided to foster the eaglet into the nest of another pair. This foster pair nested ca. 250 km away at Pawangad, Kolhapur district (16°42'N, 74°16'E), and on 5 March had two chicks in the nest.

Upon arrival on 18 March, we found the nest empty and the eagle family soaring over the nest tree. Nevertheless, we decided to place the eaglet into the vacant nest. Based on previous observations, we knew that eaglets and parents roosted at the nest for at least 2 wk after the young had fledged and that the young at this stage were still dependent on their parents for food (pers. obs.). After almost 2 hr the family was observed to land on the branches adjacent to the nest to roost for the night. Neither the young nor the parents displayed any signs of aggression toward the foster eaglet.

Initially, the family ignored the eaglet but in the evening one of the adults dropped an un-plucked chicken by the eaglet and after observing the inability of the foster eaglet to feed upon the chicken, one of the fledglings, which were ca. 60 d of age, then plucked the chicken and consumed a small portion of it. The foster eaglet observed the actions of the fledgling and imitated its movements of plucking the chicken and swallowing, and when the fledgling

left the nest, the translocated eaglet immediately grasped the partially-consumed chicken and proceeded to dismember and consume it.

For the next week (20–26 March), the parents and the fledged young alternated in bringing prey to the foster nestling. The eaglet was not observed to have any further prey handling difficulties and between feedings stood at the nest and flapped its wings vigorously. The foster chick eventually fledged on 26 March 2003.

We conclude from this episode that at least some parent Bonelli's Eagles will accept a foster young in an empty nest, but only if egg or chick loss happened a few hours earlier. We have done such translocations successfully in the past, but within 24 hr of the nest becoming empty (Pande 2003, *Newsletter for Birdwatchers* 43:31–33). Similarly, a 24-d-old chick of Changeable Hawk-Eagle (*Spizaetus cirrhatus*) has been fostered successfully in a nest of a similar species, that had been empty for just over 24 hr in India (Naoroji 1984, *J. Bombay Nat. Hist. Soc.* 82:278–308).

We assume that the finding of translocating an eaglet into a foster family during the post-fledging dependence period may also be applicable to other raptor species, provided that siblicide is not common in the host species. This technique seems mainly suitable as an emergency action to save individual birds.

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JOURNAL OF RAPTOR RESEARCH

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INDEX TO VOLUME 38

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The index includes references to general topics, common names, keywords, and authors. Reference is also made to book reviews and letters. Taxa other than raptors are included where referenced by authors.

A

Abundance, 91–95
Accipiter cooperii, 26–34, 118–124, 163–168, 250–255, 334–342
 gentilis, 243–249
 nisus, 243–249
 striatus, 62–68, 69–77, 163–168, 250–255, 334–342
Aegyptus monachus, 361–366
 Afianto, M. Yayat, see Gjershaug, Jan Ove
 Agostini, Nicolantonio, Charles Coleiro, and Michele Panuccio, Analysis of the autumn migration of juvenile honey-buzzards (*Pernis apivorus*) across the central Mediterranean, 283–286
 Agriculture, 152–157
 ALAD, 118–124
 Alaska, 81–85, 158–160, 275–277
 interior, 9–18
 Alcalde, Leandro and Sergio D. Rosset, Observation of the Chimango Caracara (*Milvago chimango*) feeding on common lesser toads (*Bufo fernandezae*), 190–191
 Aleutian archipelago, 81–85
 Alivizatos, Haralambos, Dimitris Papandropoulos, and Stamatis Zogaris, Winter diet of the Greater Spotted Eagle (*Aquila clanga*) in the Amvrakikos Wetlands, Greece, 371–374
 Alvarado, Sergio, see Pavez, Eduardo F.
 Amvrakikos, 371–374
 Amputation, 85–88
 Anthony, Robert G., see Forsman, Eric D.
 Anthony, Robert G., see Ricca, Mark A.
Aquila chrysaetos, 192, 195–207, 270–275
 clanga, 371–374
Arborimus longicaudus, 214–230
 Arctic, 158–160
 Argentina, 1–8, 152–157
 Arizona, 26–34, 238–242
 Arnello, Alejandra, see Pavez, Eduardo F.
Asio otus, 379–380
Asturina nitida, 238–242
Athene cunicularia hypugaea, 91–95
 noctua, 35–46
 Austing, G. Ronald, see Dykstra, Cheryl R.
 Avian energetics, 163–168

B

Barrett, Rowan D.H., see Sleep, Darren J.H.

Bass, Orin L., see Mealey, Brian
 Bakaloudis, Dimitris, see Vlachos, Christos
 Banding, 304–311
 Behavior, 295–303
 Bibles, Brent D. and R. William Mannan, Productivity and nest-site characteristics of Gray Hawks in southern Arizona, 238–242
 Bloise, Carolina, see Tomé, Ricardo
 Bossart, Gregory D., see Mealey, Brian
 Brandes, David and Daniel W. Ombalski, Modeling raptor migration pathways using a fluid-flow analogy, 195–207
 Brazil, southeastern, 191
 Breeding, 186–189
 biology, 1–8, 263–269
 success, 161–163, 312–319, 350–356
 Breeding Bird Atlas, 91–95
 Survey, 91–95
 Breeding conditions, 361–366
 Broerman, Fred J., see Harwood, Christopher M.
 Brood size, 361–366
 Brown, Jessi L., William R. Heinrich, J. Peter Jenny, and Brian D. Mutch, Development of hunting behavior in hacked Aplomado Falcons, 148–152
Bubo bubo, 375–377, 378–379
 scandiacus, 275–277
 Buchanan, Joseph B., Osprey scavenges Common Murre carcass in coastal Washington, 380–381
 Buchanan, Joseph B., Tracy L. Fleming, and Larry L. Irwin, A comparison of Barred and Spotted owl nest-site characteristics in the eastern Cascade Mountains, Washington, 231–237
Bufo fernandezae, 190–191
Butastur indicus, 263–269
Buteo albigula, 1–8, 186–189
 buteo, 243–249
 jamaicensis, 19–25, 181–186, 334–342
 lagopus, 181–186
 lineatus, 290, 304–311, 312–319
 swainsoni, 357–361
 Buzzard, Common, 243–249
 Grey-faced, 263–269
 Buzzard-Eagle, Black-chested, 101–102
 Byrd, Mitchell A., see Watts, Bryan D.

C

- Cage-flight exercise, 125–132
 Cangarato, Rogério, see Palma, Luís
 Cape Verde Islands, 141–147
 Caracara, Chimango, 152–157, 190–191
 Crested, 152–157
 Mountain, 290–292
Caracara plancus, 152–157
Cathartes aura, 288–289
 Creance-flight exercise, 125–132
 Chandler, Richard B., Allan M. Strong, and Carlin C. Kaufman, Elevated lead levels in urban House Sparrows: a threat to Sharp-shinned Hawks and Merlins?, 62–68
 Chatzinikos, Evangelos, see Vlachos, Christos
Chen canagica, 81–85
 Chesapeake Bay, 47–54
 Chihuahua, Mexico, 107–117
 Desert, 107–117
 Chile, central, 186–189
 Christmas Bird Count, 91–95
Circus cyaneus, 133–140, 243–249
 macroscelus, 256–262
 pygargus, 133–140
 Clarke, Michéle L., see Tingay, Ruth E.
 Cloud cover, 208–213
 Clutch size, 263–269
 Coleiro, Charles, see Agostini, Nicolantonio
 Coloniality, 350–356
 Communal roosts, 278–282
 Competition, 88–91, 178–181
 Contaminants, 69–77
 Cooperative hunting, 148–152
Coragyps atratus, 288–289
 Corbacho, Casimiro, see Villegas, Auxiliadora
 Corona, Rodrigo Sierra, see López González, Carlos A.
 Costillo, Emilio, see Villegas, Auxiliadora

D

- Daniel, F. Bernard, see Dykstra, Cheryl R.
 de Frutos, Ángel, see Olea, Pedro P.
 De Lucca, Eduardo R. see Saggese, Miguel D.
 de Roland, Lily-Arison Rene, Jeanneney Rabearivony, Ignace Randriamanga, and Russell Thorstrom, Nesting biology and diet of the Madagascar Harrier (*Circus macroscelus*) in Ambohitantely Special Reserve, Madagascar, 256–262
 Deciduous forests, 186–189
 del mar Delgado, Maria and Vincenzo Penteriani, Gender determination of Eurasian Eagle-owls (*Bubo bubo*) by morphology, 375–377
 DeLong, John P., and Stephen W. Hoffman, Fat stores of migrant Sharp-shinned and Cooper's hawks in New Mexico, 163–168
 Deng, Wen-Hong, Wei Gao, and Jiang Zhao, Breeding

biology of the Grey-faced Buzzard (*Butastur indicus*) in northeastern China, 263–269

- Development, 263–269
 Discriminant function analysis, 375–377
 Diet, 69–77, 178–181, 214–230, 256–262, 371–374
 Dietary shift, 174–177
 Dispersal, 26–34
 Distribution, 107–117, 181–186
 Disturbance response, 295–303
 Dominance hierarchy, 85–88
 Domínguez, Jesús, see Tapia, Luis
 Double brooding, 378–379
 Dykstra, Cheryl R., Jeffery L. Hays, Melinda M. Simon, John B. Holt, Jr., G. Ronald Austing, and F. Bernard Daniel, Dispersal and mortality of Red-shouldered Hawks banded in Ohio, 304–311

E

- Eagle, Bald, 81–85, 96–100, 295–303
 Bonelli's, 381–382
 Booted, 168–174
 Golden, 192, 195–207, 270–275
 Greater Spotted, 371–374
 Eagle-Owl, Eurasian, 375–377, 378–379
 Ecomorphology, 334–342
Elanus leucurus, 178–181
 Ellis, David H. and Marc Kéry, Variable retention times for retrices at different loci in a Golden Eagle, 270–275
 Engelmann, Mathias, see Greene, Dana M.
 Estes, Wendy A., see Mannan, R. William
 Everglades, 96–100
 Exercise cage-flight, 125–132
 creance-flight, 125–132

F

- Falco cherrug*, 292–293
 columbarius, 62–68
 eleonora, 320–325
 femoralis, 107–117, 148–152
 naumanni, 161–163, 278–282
 peregrinus, 9–18, 158–160
 sparverius, 250–255, 334–342
 subbuteo, 287–288
 Falcon, Aplomado, 107–117, 148–152
 Eleonora's, 292–293, 320–325
 Peregrine, 9–18, 158–160
 Saker, 292–293
 Sooty, 292–293
 False eyes, 287
 Fat scores, 163–168
 stores, 163–168
 Ferguson, Howard L., Relative abundance and diversity

- of winter raptors in Spokane County, eastern Washington, 181–186
- Ferreira, João, see Palma, Luís
- Finland, 243–249
- Fire perturbations, 174–177
- Fish-Eagle, Madagascar, 85–88
- Fish farms, 326–333
 - predation, 326–333
- Fitness, male, 320–325
 - muscle, 125–132
- Fish-Owl, Tawny, 326–333
- Fledgling sex ratio, 361–366
- Fledglings, 161–163, 263–269
- Fleming, Tracy L., see Buchanan, Joseph B.
- Florida, 55–61, 96–100
 - Bay, 96–100
- Food habits, 81–85
- Forearm, 375–377
- Foraging behavior, 148–152
 - theory, 9–18
- Forsman, Eric D., Robert G. Anthony, E. Charles Meslow, and Cynthia J. Zabel, Diets and foraging behavior of northern Spotted Owls in Oregon, 214–230
- Fostering nestlings, 381–382
- Fundy National Park, 69–77

G

- Gabella, Juan P., see Pavez, Eduardo F.
- Gao, Wei, see Deng, Wen-Hong
- García Dios, Ignacio S., Spanish ringing and recovery records of Booted Eagle (*Hieraaetus pennatus*), 168–174
- García-Ripollés, Clara, see López-López, Pascual
- Gelain, Mariano, see Trejo, Ana
- Gender determination, 357–361, 375–377
- Genetic variation, 250–255
- Geranoaetus melanoleucus*, 101–102
- Giving-up time, 19–25
- Gjershaug, Jan Ove, Nils Røv, Torgeir Nygård, Dewi M. Prawiradilaga, M. Yayat Afianto, Hapsoro, and Adam Supriatna, Home range size of the Javan Hawk-Eagle (*Spizaetus bartelsi*) estimated from direct observations and radiotelemetry, 343–349
- Glaucornis sabrinus*, 214–230
- Goose, Emperor, 81–85
- Goldstein, Michael I. and Toby J. Hibbitts, Summer roadside raptor surveys in the western pampas of Argentina, 152–157
- González, Benito A., see Pavez, Eduardo F.
- González, Christian, see Pavez, Eduardo F.
- Goshawk, Northern, 243–249
- Grande, Juan Manuel, see Negro, Juan José
- Greene, Dana M., Mathias Engelmann, and Todd R. Steck, An assessment of cage flight as an exercise method for raptors, 125–132
- Granzinoli, Marco Antonio Monteiro, see Motta-Junior, José Carlos

- Graves, Gary R., Commensal foraging by a Red-shouldered Hawk (*Buteo lineatus*) with Wild Turkeys (*Meleagris gallopavo*), 290
- Greece, 371–374
- Griffon, Eurasian, 350–356
- Gross, Howard P., see McBride, Tobias J.
- Grouse, 243–249
- Guevara, Eduardo Ponce, see López González, Carlos A.
- Guyer, Craig, see Ress, Sara
- Gyps fulvus*, 350–356

H

- Habitat, 158–160, 231–237
 - selection, 26–34, 35–46
 - use, 133–140
- Hacking, 148–152
- Haliaeetus leucocephalus*, 81–85, 96–100, 295–303
 - vociferoides*, 85–88
- Hapsoro, see Gjershaug, Jan Ove
- Harrier, Hen, 133–140
 - Madagascar, 256–262
 - Montagu's, 133–140
 - Northern, 243–249
- Harwood, Christopher M., Brian J. McCaffery, Fred J. Broerman, and Paul A. Liedberg, A local concentration of Snowy Owls in the Yukon-Kuskokwim Delta in Summer 2000, 275–277
- Hawk, Cooper's, 26–34, 118–124, 163–168, 250–255, 334–342
 - Gray, 238–242
 - Red-shouldered, 290, 304–311, 312–319
 - Red-tailed, 19–25, 181–186, 334–342
 - Rough-legged, 181–186
 - Sharp-shinned, 62–68, 69–77, 163–168, 250–255, 334–342
 - Swainson's, 357–361
 - White-tailed, 191
 - White-throated, 1–8, 186–189
- Hawk-Eagle, Javan, 343–349
 - Ornate, 193–194
- Hays, Jeffery L., see Dykstra, Cheryl R.
- Health assessment, 96–100
- Heinrich, William R., see Brown, Jessi L.
- Hematology, 96–100
- Hibbitts, Toby J., see Goldstein, Michael I.
- Hieraaetus fasciatus*, 381–382
 - pennatus*, 168–174
- Hobby, Eurasian, 287–288
- Hoffman, Stephen W., A review of raptors of eastern North America, by Brian K. Wheeler, 2003, 103–104
- Hoffman, Stephen W., see DeLong, John P.
- Holt, Jr., John B., see Dykstra, Cheryl R.
- Home range, 238–242, 343–349
 - size, 26–34
- Honey-buzzard, European, 283–286
 - Oriental, 367–371

- Hooper, Michael J., see McBride, Tobias J.
 Huang, Kuang-Ying, Yao-Sung Lin, and Lucia Liu Severinghaus, Nest provisioning of the Oriental Honey-buzzard (*Pernis ptilorhynchus*) in northern Taiwan, 367–371
 Huhtala, Kauko, see Reif, Vitali
 Human activity, 295–303
 Hungary, 292–293
 Hunting, 19–25
 behavior, 148–152
 cooperative, 292–293

I

- Indonesia, 343–349
 Injury, 77–81
 Insect hawking, 379–380
 Iverson, Wayne F., Reproductive success of Spotted Owls sympatric with Barred Owls in western Washington, 88–91
 Irwin, Larry L, see Buchanan, Joseph B.

J

- Jenny, J. Peter, see Brown, Jessi L.

K

- Kalavah, Loukman, see Tingay, Ruth E.
 Kaufman, Carlin C., see Chandler, Richard B.
 Kéry, Marc, see Ellis, David H.
 Kestrel, American, 250–255, 334–342
 Lesser, 161–163, 278–282
Ketupa flavipes, 326–333
 Kingfisher, Ringed, 191
 Kirk, David Anthony, see Woodley, Stephen J.
 Kite, White-tailed, 178–181
 Korpimäki, Erkki, see Tomé, Ricardo

L

- Lead, 62–68, 118–124
 Lehman, Chad P. and Dan J. Thompson, Golden Eagle (*Aquila chrysaetos*) predation attempts on Merriam's Turkeys (*Meleagris gallopavo merriami*) in the southern Black Hills, South Dakota, 192
 Leyhe, Jennifer E. and Gary Ritchison, Perch sites and hunting behavior of Red-tailed Hawks (*Buteo jamaicensis*), 19–25
 Leveau, Carlos M., see Leveau, Lucas M.
 Leveau, Lucas M., Carlos M. Leveau, and Ulyses F.J. Pardiñas, Trophic relationships between White-tailed Kites (*Elanus leucurus*) and Barn Owls (*Tyto alba*) in southern Buenos Aires Province, Argentina, 178–181
 Liedberg, Paul A., see Harwood, Christopher M.
 Lin, Yao-Sung, see Huang, Kuang-Ying
 Longevity, 85–88, 168–174
 López González, Carlos A., Eduardo Ponce Guevara, Karla Pelz Serrano, Hugo Luna Soria, and Rodrigo Si-

- erra Corona, A record of the Ornate Hawk-Eagle (*Spizaetus ornatus*) in Nayarit, Mexico, 193–194
 López-López, Pascual, Clara García-Ripollés, and José Verdejo, Population status and reproductive performance of Eurasian Griffons (*Gyps fulvus*) in eastern Spain, 350–356
 Lunar phase, 208–213

M

- Madagascar, 256–262
 Mahabal, Anil, see Pande, Satish A.
 Male fitness, 320–325
 Mannan, R. William, Wendy A. Estes, and William J. Matter, Movements and survival of fledgling Cooper's Hawks in an urban environment, 26–34
 Mannan, R. William, see Bibles, Brent D.
 Martell, Mark S., Michael A. McMillian, Mathew J. Solen-sky, and Brian K. Mealey, Partial migration and wintering use of Florida by Ospreys, 55–61
 Martin, Elwood (Woody) M., Decreases in a population of Red-shouldered Hawks nesting in central Maryland, 312–319
 Maryland, central, 312–319
 Matter, William J., see Mannan, R. William McBride, Tobias J., Jeff P. Smith, Howard P. Gross, and Michael J. Hooper, Blood-lead and ALAD-activity levels of Cooper's Hawks (*Accipiter cooperii*) migrating through the southern Rocky Mountains, 118–124
 McCaffery, Brian J., see Harwood, Christopher M.
 McIntyre, Nancy E., Historical and current status of breeding and wintering western Burrowing Owls (*Athene cunicularia hypugaea*) in Texas, 91–95
 McMillian, Michael A., see Martell, Mark S.
 Mealey, Brian, Greta M. Parks, Carlos M. Pages, Brian A. Millsap, Orin L. Bass, and Gregory D. Bossart, Serum chemistry values for nestling Bald Eagles (*Haliaeetus leucocephalus*) in Florida Bay, Everglades National Park, 96–100
 Mealey, Brian K., see Martell, Mark S.
 Mediterranean region, 35–46
Meleagris gallopavo, 290
 Merlin, 62–68
 Meslow, E. Charles, see Forsman, Eric D.
 Mesquite, 152–157
 Mexico, Chihuahua, 107–117
 Nayarit, 193–194
 Meyer, Kenneth D., see Woodley, Stephen J.
 Migration, 55–61, 62–68, 118–124, 163–168, 195–207, 283–286, 334–342
 Millier, Carl, see Eakle, Wade L.
 Millsap, Brian A., see Mealey, Brian
Milvago chimango, 152–157, 190–191
 Mineau, Pierre, see Eakle, Wade L.
 Mitochondrial DNA, 250–255
 Modeling, 133–140, 195–207
 Molecular sexing, 320–325, 357–361

Molt, 270–275
 Montoya, Angel B., see Young, Kendal E.
 Morán, Ricardo, see Villegas, Auxiliadora
 Morphometric measures, 357–361
 Mortality, 168–174, 326–333
 factor, 77–81
 Motta-Junior, José Carlos and Marco Antonio Monteiro
 Granzinoli, Consumption of a Ringed Kingfisher
 (*Megaceryle torquata*) by a White-tailed Hawk (*Buteo
 albicaudatus*) in southeastern Brazil, 191
 Mutch, Brian D., see Brown, Jessi L.
 Murre, Common, 380–381

N

Natal dispersal, 304–311
 Negro, Juan José, Juan Manuel Grande, and José Hernán
 Sarasola, Do Eurasian Hobbies (*Falco subbuteo*) have
 “false eyes” on the nape?, 287–288
 Negro, Juan José, see Sarasola, José Hernán
 Nest characteristics, 238–242
 provisioning, 367–371
 sites, 231–237
 substrate, 47–54
 Nesting, 161–163
 behavior, 256–262
 Nestling diet, 9–18
 provisioning rates, 9–18
 Nestlings, 263–269
 Nests, 1–8, 256–262
 New Brunswick, 69–77
 Nordmeyer, Dana L., see Palmer, Angela G.
 Northern flying squirrel, 214–230
 Nygård, Torgeir, see Gjershaug, Jan Ove

O

Ojeda, Valeria, see Trejo, Ana
 Olea, Pedro P., Rubén Vera, Ángel de Frutos, and Hugo
 Robles, Premigratory communal roosts of the Lesser
 Kestrel in the boreal summer, 278–282
 Ombalski, Daniel W., see Brandes, David
 Orellana, Sergio Alvarado, see Rojas, Ricardo Figueroa
 Orientation, 283–286
 Osprey, 47–54, 55–61, 141–147, 380–381
 Ortego, Joaquín, A possible case of double-brooding of
 Eagle-Owls (*Bubo bubo*) in Spain, 378–379
 Owl, Barn, 174–177, 17–181
 Barred, 88–91, 231–237
 Little, 35–46
 Long-eared, 379–380
 Northern Spotted, 88–91, 214–230, 231–237
 Snowy, 275–277
 Western Burrowing, 91–95

P

Palma, Luís, João Ferreira, Rogério Cangarato, and Pe-

dro Vaz Pinto, Current status of the Osprey in the
 Cape Verde Islands, 141–147
 Palmer, Angela G., Dana L. Nordmeyer, and Daniel D.
 Roby, Nestling provisioning rates of Peregrine Fal-
 cons in interior Alaska, 9–18
 Pande, Satish A., Amit P. Pawashe, Banda Pednekar, Anil
 Mahabal, and Reuven Yosef, How long is too long?
 A case of fostering nestling Bonelli's Eagles (*Hieraee-
 tus fasciatus*), 381–382
Pandion haliaetus, 47–54, 55–61, 141–147, 380–381
 Panuccio, Michele, see Agostini, Nicolantonio
 Papandropoulos, Dimitris, see Alivizatos, Haralambos
 Pages, Carlos M., see Mealey, Brian
 Paper wasps, 367–371
Parapolybia, 367–371
 Pardiñas, Ulyses F.J., see Leveau, Lucas M.
 Parks, Greta M., see Mealey, Brian
Passer domesticus, 62–68
 Patagonia, 174–177
 northwestern, 1–8
 Pathways, 195–207
 Pavez, Eduardo F., Christian González, Benito A. Gonzá-
 lez, Cristián Saucedo, Sergio Alvarado, Juan P. Ga-
 bella, and Alejandra Arnello, Nesting of the White-
 throated Hawk (*Buteo albigula*) in deciduous forests
 of central Chile, 186–189
 Pawashe, Amit P., see Pande, Satish A.
 Pb, 62–68
 Pearce, Peter A., see Woodley, Stephen J.
 Pearlstine, Elise V., Variation in mitochondrial DNA of
 four species of migratory raptors, 250–255
 Pearlstine, Elise Vernon and Daniel B. Thompson, Geo-
 graphic variation in morphology of four species of
 migratory raptors, 334–342
 Pednekar, Banda, see Pande, Satish A.
 Pentriani, Vincenzo, see Del Mar Delgado, Maria
 Perch site, 19–25
Pernis apivorus, 283–286
 ptilorhynchus, 367–371
Phalcoboenus megalopterus, 290–292
 Philopatry, 168–174
 Plumage, 270–275
Polistes, 367–371
 Population declines, 69–77, 312–319
 increase, 47–54
 status, 343–349
 trend, 91–95
 Prawiradilaga, Dewi M., see Gjershaug, Jan Ove
 Predation, 243–249
 risk, 35–46
 Premigratory aggregations, 278–282
 Prey selection, 214–230
 Principal components analysis, 334–342
 Productivity, 238–242, 350–356

R

Rabearivony, Jeanneney, see de Roland, Lily-Arison Rene

- Randriamanga, Ignace, see de Roland, Lily-Arison Rene
 Radio-tracking, 343–349
 Raptor rehabilitation, 77–81, 125–132
 Red tree vole, 214–230
 Relative abundance, 181–186
 Release, 77–81
 Reproductive success, 35–46, 263–269
 Ress, Sara and Craig Guyer, A retrospective study of mortality and rehabilitation of raptors in the southeastern United States, 77–81
 RFLP, 250–255
 Ricca, Mark A., Robert G. Anthony, and Jeffrey C. Williams, Bald Eagles consume Emperor Geese during late-winter in the Aleutian archipelago, 81–85
 Rief, Vitali, Risto Tornberg, and Kauko Huhtala, Juvenile grouse in the diet of some raptors, 243–249
 Ristow, Dietrich and Michael Wink, Seasonal variation in sex ratio of nestling Eleonora's Falcons, 320–325
 Ritchie, Robert J., Ann M. Wildman, and Clayton M. White, Peregrine Falcons nesting on lake bluffs on the Arctic coastal plain of northern Alaska, 158–160
 Ritchison, Gary, see Leyhe, Jennifer E.
 Roadside survey, 181–186
 Robles, Hugo, see Olea, Pedro P.
 Roby, Daniel D., see Palmer, Angela G.
 Roen, Keely T. and Richard H. Yahner, Vulture winter roost abandonment and reestablishment, 288–289
 Rodriguez, Luis, see Tapia, Luis
 Rojas, Ricardo Figueroa, Sergio Alvarado Orellana, and E. Soraya Corales Stappung, Notes on a range expansion and summer diet of the Mountain Caracara in the Andes of south-central Chile, 290–292
 Rosset, Sergio D., see Alcalde, Leandro
 Røv, Nils, see Gjershaug, Jan Ove

S

- Saggese, Miguel D. and Eduardo R. De Lucca, Live mammal prey (*Zaedyus pichiy*) in a nest of the Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*), 101–102
 Sahoresh, Mercedes and Ana Trejo, Diet shift of Barn Owls (*Tyto alba*) after natural fires in Patagonia, Argentina, 174–177
 Sánchez-Guzmán, Juan Manuel, see Villegas, Auxiliadora
 Sarasola, José Hernán and Juan José Negro, Gender determination in the Swainson's Hawk (*Buteo swainsoni*) using molecular procedures and discriminant function analysis, 357–361
 Sarasola, José Hernán, see Negro, Juan José
 Satellite telemetry, 55–61
 Saucedo, Cristián, see Pavez, Eduardo F.
 Scavenging, 380–381
 Schmutz, Josef K., A review of a hawk in the sun: adventures studying hawks, by Leon R. Powers, 2003, 294
 Seavy, Nathaniel E., Environmental correlates of African Wood-Owl calling activity in Kibale National Park, Uganda, 208–213

- Serum chemistry, 96–100
 Serrano, Karla Pelz, see López González, Carlos A.
 Severinghaus, Lucia Liu, see Huang, Kuang-Ying
 Sex allocation, 320–325
 ratio, 320–325
 Sexing, 375–377
 Sexual dimorphism, 361–366
 Simon, Melinda M., see Dykstra, Cheryl R.
 Sleep, Darren J.H. and Rowan D.H. Barrett, Insect hawking observed in the Long-eared Owl (*Asio otus*), 379–380
 Smith, Jeff P., see McBride, Tobias J.
 Solensky, Mathew W., see Martell, Mark S.
 Soria, Hugo Luna, see López González, Carlos A.
 Spain, 133–140, 350–356, 361–366, 378–379
 Sparrow, House, 62–68
 Sparrowhawk, Eurasian, 243–249
Spizaetus bartelsi, 343–349
 ornatus, 193–194
 Stappung, E. Soraya Corales, see Rojas, Ricardo Figueroa
 Status, 141–147
 Steck, Todd R., see Greene, Dana M.
 Strong, Allan M., see Chandler, Richard B.
Strix occidentalis caurina, 88–91, 214–230, 231–237
 varia varia, 88–91, 231–237
 woodfordii, 208–213
 Sun, Yuan-Hsun, Hsin-Ju Wu, and Ying Wang, Tawny Fish-Owl predation at fish farms in Taiwan, 326–333
 Supriatna, Adam, see Gjershaug, Jan Ove
 Survey, 141–147, 152–157, 158–160, 181–186, 208–213
 Sympatry, 181–186
 Simpson, Lorenzo, see Trejo, Ana
 Survival, 304–311

T

- Taiwan, 326–333, 367–371
 Tapia, Luis, Jesús Domínguez, and Luis Rodríguez, Modeling habitat use and distribution of Hen Harriers (*Circus cyaneus*) and Montagu's Harrier (*Circus pygargus*) in a mountainous area in Galicia, northwestern Spain, 133–140
 Terrain, 195–207
 Terrazas, Alberto Lafón, see Young, Kendal E.
 Texas, 91–95, 148–152
 Thompson, Bruce C., see Young, Kendal E.
 Thompson, Dan J., see Lehman, Chad P.
 Thompson, Daniel B., see Pearlstine, Elise Vernon
 Thorstrom, Russell, see de Roland, Lily-Arison Rene
 Thorstrom, Russell, see Tingay, Ruth E.
 Tingay, Ruth E., Michèle L. Clarke, Richard T. Watson, Russell Thorstrom, and Loukman Kalavah, Survival and behavior of a one-footed Madagascar Fish-Eagle in the wild, 85–88
 Tomé, Ricardo, Carolina Bloise, and Erkki Korpimäki, Nest-site selection and nesting success of Little Owls (*Athene noctua*) in Mediterranean woodland and open habitats, 35–46

Tornberg, Risto, see Reif, Vitali
 Toxicology, 118–124
 Trejo, Ana, Valeria Ojeda, Lorenzo Simpson, and Mariano Gelain. Breeding biology and nest characteristics of the White-throated Hawk (*Buteo albigula*) in northwestern Argentine Patagonia, 1–8
 Trejo, Ana, see Sahores, Mercedes
 Trophic overlap, 178–181
 Tucson, Arizona, 26–34
Tyto alba, 174–177, 178–181

U

Updraft, 195–207
 Uganda, 208–213
 Urban, 304–311
 ecosystem, 62–68
 environments, 26–34
Uria aalge, 380–381

V

Valdez, Raul, see Young, Kendal E.
 Vaz Pinto, Pedro, see Palma Luís
 Vera, Rubén, see Olea, Pedro P.
 Verdejo, José, see López-López, Pascual
 Világosi, János, see Eakle, Wade L.
 Villegas, Auxiliadora, Juan Manuel Sánchez-Guzmán, Emilio Costillo, Casimiro Corbacho, and Ricardo Morán. Productivity and fledgling sex ratio in a Cinereous Vulture (*Aegypius monachus*) population in Spain, 361–366
 Vlachos, Christos, Dimitris Bakaloudis, and Evangelos Chatzinikos. Unusual nesting of the Lesser Kestrel (*Falco naumanni*) in Thessaly, Greece, 161–163
 Vocalizations, 208–213
 Vulture, Black, 288–289
 Cinereous, 361–366
 Turkey, 288–289
 restaurants, 350–356

W

Wang, Ying, see Sun, Yuan-Hsun

Washington, 88–91, 231–237, 295–303
 Water-crossing, 283–286
 Watson, James W., Responses of nesting Bald Eagles to experimental pedestrian activity, 295–303
 Watson, Richard T., see Tingay, Ruth E.
 Watts, Bryan D., Mitchell A. Byrd, and Marian U. Watts. Status and distribution of breeding Ospreys in the Chesapeake Bay: 1995–1996, 47–54
 Watts, Marian U., see Watts, Bryan D.
 Wetland, 371–374
 White, Clayton M., see Ritchie, Robert J.
 Wildman, Ann M., see Ritchie, Robert J.
 Williams, Jeffrey C., see Ricca, Mark A.
 Wink, Michael, see Ristow, Dietrich
 Winter, 371–376
 distribution, 181–186
 Wintering area, 55–61
 grounds, 357–361
 Wood-Owl, African, 208–213
 Woodley, Stephen J., Kenneth D. Meyer, David Anthony Kirk, and Peter A. Pearce. Contaminant levels, egg-shell thinning, and productivity in Sharp-shinned Hawks in Fundy National Park, New Brunswick, 69–77
 Wu, Hsin-Ju, see Sun, Yuan-Hsun

Y

Yahner, Richard H., see Roen, Keely T.
 Yosef, Reuven, see Pande, Satish A.
 Young, Kendal E., Bruce C. Thompson, Alberto Lafón Terrazas, Angel B. Montoya, and Raul Valdez. Aplomado Falcon abundance and distribution in the northern Chihuahuan Desert of Mexico, 107–117
 Yukon Delta National Wildlife Refuge, 275–277
 Yukon-Kuskokwim Delta, 275–277

Z

Zabel, Cynthia J., see Forsman, Eric D.
Zaedyus pichiy, 101–102
 Zhao, Jiang, see Deng, Wen-Hong
 Zogaris, Stamatis, see Alivizatos, Haralambos

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CONTENTS FOR VOLUME 38, 2004

NUMBER 1

BREEDING BIOLOGY AND NEST CHARACTERISTICS OF THE WHITE-THROATED HAWK (<i>BUTEO ALBIGULA</i>) IN NORTHWESTERN ARGENTINE PATAGONIA. Ana Trejo, Valeria Ojeda, Lorenzo Sympson, and Mariano Gelain	1
NESTLING PROVISIONING RATES OF PEREGRINE FALCONS IN INTERIOR ALASKA. Angela G. Palmer, Dana L. Nordmeyer, and Daniel D. Roby	9
PERCH SITES AND HUNTING BEHAVIOR OF RED-TAILED HAWKS (<i>BUTEO JAMAICENSIS</i>). Jennifer E. Leyhe and Gary Ritchison	19
MOVEMENTS AND SURVIVAL OF FLEDGLING COOPER'S HAWKS IN AN URBAN ENVIRONMENT. R. William Mannan, Wendy A. Estes, and William J. Matter.....	26
NEST-SITE SELECTION AND NESTING SUCCESS OF LITTLE OWLS (<i>ATHENE NOCTUA</i>) IN MEDITERRANEAN WOODLAND AND OPEN HABITATS. Ricardo Tomé, Carolina Bloise, and Erkki Korpimäki.....	35
STATUS AND DISTRIBUTION OF BREEDING OSPREYS IN THE CHESAPEAKE BAY: 1995—96. Bryan D. Watts, Mitchell A. Byrd, and Marian U. Watts	47
PARTIAL MIGRATION AND WINTERING USE OF FLORIDA BY OSPREYS. Mark S. Martell, Michael A. McMillian, Mathew J. Solensky, and Brian K. Mealey	55
ELEVATED LEAD LEVELS IN URBAN HOUSE SPARROWS: A THREAT TO SHARP-SHINNED HAWKS AND MERLINS? Richard B. Chandler, Allan M. Strong, and Carlin C. Kaufman	62
SHORT COMMUNICATIONS	
CONTAMINANT LEVELS, EGGSHELL THINNING, AND PRODUCTIVITY IN SHARP-SHINNED HAWKS IN FUNDY NATIONAL PARK, NEW BRUNSWICK. Stephen J. Woodley, Kenneth D. Meyer, David Anthony Kirk, and Peter A. Pearce	69
A RETROSPECTIVE STUDY OF MORTALITY AND REHABILITATION OF RAPTORS IN THE SOUTHEASTERN UNITED STATES. Sara Ress and Craig Guyer	77
BALD EAGLES CONSUME EMPEROR GEESE DURING LATE-WINTER IN THE ALEUTIAN ARCHIPELAGO. Mark A. Ricca, Robert G. Anthony, and Jeffrey C. Williams	81
SURVIVAL AND BEHAVIOR OF A ONE-FOOTED MADAGASCAR FISH-EAGLE IN THE WILD. Ruth E. Tingay, Michèle L. Clarke, Richard T. Watson, Russell Thorstrom, and Loukman Kalavah	85
REPRODUCTIVE SUCCESS OF SPOTTED OWLS SYMPATRIC WITH BARRED OWLS IN WESTERN WASHINGTON. Wayne F. Iverson	88
HISTORICAL AND CURRENT STATUS OF BREEDING AND WINTERING WESTERN BURROWING OWLS (<i>ATHENE CUNICULARIA HYPUGAEA</i>) IN TEXAS. Nancy E. McIntyre	91
SERUM CHEMISTRY VALUES FOR NESTLING BALD EAGLES (<i>HALIAEETUS LEUCOCEPHALUS</i>) IN FLORIDA BAY, EVERGLADES NATIONAL PARK. Brian Mealey, Greta M. Parks, Carlos M. Pages, Brian A. Millsap, Orin L. Bass, and Gregory D. Bossart	96
LETTER	
LIVE MAMMAL PREY (<i>ZAEDYUS PICHII</i>) IN A NEST OF THE BLACK-CHESTED BUZZARD-EAGLE (<i>GERANOAEETUS MELANOLEUCUS</i>). Miguel D. Saggese and Eduardo R. De Lucca	101

BOOK REVIEW. Edited by Jeffrey S. Marks	103
MANUSCRIPT REFEREES	105

NUMBER 2

APLOMADO FALCON ABUNDANCE AND DISTRIBUTION IN THE NORTHERN CHIHUAHUAN DESERT OF MEXICO. Kendal E. Young, Bruce C. Thompson, Alberto Lafón Terrazas, Angel B. Montoya, and Raul Valdez	107
BLOOD-LEAD AND ALAD ACTIVITY LEVELS OF COOPER’S HAWKS (<i>ACCIPITER COOPERII</i>) MIGRATING THROUGH THE SOUTHERN ROCKY MOUNTAINS. Tobias J. McBride, Jeff P. Smith, Howard P. Gross, and Michael J. Hooper	118
AN ASSESSMENT OF CAGE FLIGHT AS AN EXERCISE METHOD FOR RAPTORS. Dana M. Greene, Mathias Engelmann, and Todd R. Steck	125
MODELING HABITAT USE AND DISTRIBUTION OF HEN HARRIERS (<i>CIRCUS CYANEUS</i>) AND MONTAGU’S HARRIER (<i>CIRCUS PYGARGUS</i>) IN A MOUNTAINOUS AREA IN GALICIA, NORTHWESTERN SPAIN. Luis Tapia, Jesús Domínguez, and Luis Rodríguez	133
CURRENT STATUS OF THE OSPREY IN THE CAPE VERDE ISLANDS. Luís Palma, João Ferreira, Rogério Cangarato, and Pedro Vaz Pinto	141
SHORT COMMUNICATIONS	
DEVELOPMENT OF HUNTING BEHAVIOR IN HACKED APLOMADO FALCONS. Jessi L. Brown, William R. Heinrich, J. Peter Jenny, and Brian D. Mutch	148
SUMMER ROADSIDE RAPTOR SURVEYS IN THE WESTERN PAMPAS OF ARGENTINA. Michael I. Goldstein and Toby J. Hibbitts	152
PEREGRINE FALCONS NESTING ON LAKE BLUFFS ON THE ARCTIC COASTAL PLAIN OF NORTHERN ALASKA. Robert J. Ritchie, Ann M. Wildman, and Clayton M. White	158
UNUSUAL NESTING OF THE LESSER KESTREL (<i>FALCO NAUMANNI</i>) IN THESSALY, GREECE. Christos Vlachos, Dimitris Bakaloudis, and Evangelos Chatzinikos	161
FAT STORES OF MIGRANT SHARP-SHINNED AND COOPER’S HAWKS IN NEW MEXICO. John P. DeLong and Stephen W. Hoffman	163
SPANISH RINGING AND RECOVERY RECORDS OF BOOTED EAGLE (<i>HIERAATUS PENNATUS</i>). IGNACIO S. GARCÍA DIOS.....	168
DIET SHIFT OF BARN OWLS (<i>TYTO ALBA</i>) AFTER NATURAL FIRES IN PATAGONIA, ARGENTINA. Mercedes Sahores and Ana Trejo.....	174
TROPHIC RELATIONSHIPS BETWEEN WHITE-TAILED KITES (<i>ELANUS LEUCURUS</i>) AND BARN OWLS (<i>TYTO ALBA</i>) IN SOUTHERN BUENOS AIRES PROVINCE, ARGENTINA. Lucas M. Leveau, Carlos M. Leveau, and Ulyses F.J. Pardiñas	178
RELATIVE ABUNDANCE AND DIVERSITY OF WINTER RAPTORS IN SPOKANE COUNTY, EASTERN WASHINGTON. Howard L. Ferguson	181
NESTING OF THE WHITE-THROATED HAWK (<i>BUTEO ALBIGULA</i>) IN DECIDUOUS FORESTS OF CENTRAL CHILE. Eduardo F. Pavez, Christian González, Benito A. González, Cristián Saucedo, Sergio Alvarado, Juan P. Gabella, and Alejandra Arnello	186
LETTERS	
OBSERVATION OF THE CHIMANGO CARACARA (MILVAGO CHIMANGO) FEEDING ON COMMON LESSER TOADS (<i>BUFO FERNANDEZAE</i>). Leandro Alcalde and Sergio D. Rosset	190
CONSUMPTION OF A RINGED KINGFISHER (<i>MEGACERYLE TORQUATA</i>) BY A WHITE-TAILED HAWK (<i>BUTEO ALBICAUDATUS</i>) IN SOUTHEASTERN BRAZIL. José Carlos Motta-Junior and Marco Antonio Monteiro Granzinolli	191
GOLDEN EAGLE (<i>AQUILA CHRYSAETOS</i>) PREDATION ATTEMPTS ON MERRIAM’S TURKEYS (<i>MELEAGRIS GALLPAVO MERRIAMI</i>) IN THE SOUTHERN BLACK HILLS, SOUTH DAKOTA. Chad P. Lehman and Dan J. Thompson	192

A RECORD OF THE ORNATE HAWK-EAGLE (<i>SPIZAETUS ORNATUS</i>) IN NAYARIT, MEXICO. Carlos A. López González, Eduardo Ponce Guevara, Karla Pelz Serrano, Hugo Luna Soria, and Rodrigo Sierra Corona	193
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NUMBER 3

MODELING RAPTOR MIGRATION PATHWAYS USING A FLUID-FLOW ANALOGY. David Brandes and Daniel W. Ombalski	195
ENVIRONMENTAL CORRELATES OF AFRICAN WOOD-OWL CALLING ACTIVITY IN KIBALE NATIONAL PARK, UGANDA. Nathaniel E. Seavy	208
DIETS AND FORAGING BEHAVIOR OF NORTHERN SPOTTED OWLS IN OREGON. Eric D. Forsman, Robert G. Anthony, E. Charles Meslow, and Cynthia J. Zabel	214
A COMPARISON OF BARRED AND SPOTTED OWL NEST-SITE CHARACTERISTICS IN THE EASTERN CASCADE MOUNTAINS, WASHINGTON. Joseph B. Buchanan, Tracy L. Fleming, and Larry L. Irwin	231
PRODUCTIVITY AND NEST-SITE CHARACTERISTICS OF GRAY HAWKS IN SOUTHERN ARIZONA. Brent D. Bibles and R. William Mannan	238
JUVENILE GROUSE IN THE DIET OF SOME RAPTORS. Vitali Reif, Risto Tornberg, and Kauko Huhtala	243
VARIATION IN MITOCHONDRIAL DNA OF FOUR SPECIES OF MIGRATORY RAPTORS. Elise V. Pearlstine	250
NESTING BIOLOGY AND DIET OF THE MADAGASCAR HARRIER (<i>CIRCUS MACROSCELES</i>) IN AMBOHITANTELY SPECIAL RESERVE, MADAGASCAR. Lily-Arison Rene de Roland, Jeanneney Rabearivony, Ignace Randriamanga, and Russell Thorstrom	256
BREEDING BIOLOGY OF THE GREY-FACED BUZZARD (<i>BUTASTUR INDICUS</i>) IN NORTHEASTERN CHINA. Wen-Hong Deng, Wei Gao, and Jiang Zhao	263

SHORT COMMUNICATIONS

VARIABLE RETENTION TIMES FOR RECTRICES AT DIFFERENT LOCI IN A GOLDEN EAGLE. David H. Ellis and Marc Kéry	270
A LOCAL CONCENTRATION OF SNOWY OWLS ON THE YUKON-KUSKOKWIM DELTA IN SUMMER 2000. Christopher M. Harwood, Brian J. McCaffery, Fred J. Broerman, and Paul A. Liedberg	275
PREMIGRATORY COMMUNAL ROOSTS OF THE LESSER KESTREL IN THE BOREAL SUMMER. Pedro P. Olea, Rubén Vera, Ángel de Frutos, and Hugo Robles	278
ANALYSIS OF THE AUTUMN MIGRATION OF JUVENILE HONEY-BUZZARDS (<i>PERNIS APIVORUS</i>) ACROSS THE CENTRAL MEDITERRANEAN. Nicolantonio Agostini, Charles Coleiro, and Michele Panuccio	283

LETTERS

DO EURASIAN HOBBIES (<i>FALCO SUBBUTEO</i>) HAVE “FALSE EYES” ON THE NAPE? Juan José Negro, Juan Manuel Grande, and José Hernán Sarasola	287
VULTURE WINTER ROOST ABANDONMENT AND REESTABLISHMENT. Keely T. Roen and Richard H. Yahner	288
COMMENSAL FORAGING BY A RED-SHOULDERED HAWK (<i>BUTEO LINEATUS</i>) WITH WILD TURKEYS (<i>MELEAGRIS GALLOPAVO</i>). Gary R. Graves	290
NOTES ON A RANGE EXPANSION AND SUMMER DIET OF THE MOUNTAIN CARACARA IN THE ANDES OF SOUTH-CENTRAL CHILE. Ricardo Figueroa Rojas, Sergio Alvarado Orellana, and E. Soraya Corales Stappung	290

AN EXAMPLE OF COOPERATIVE HUNTING BY SAKER FALCONS IN HUNGARY. Wade L. Eakle, Carl Millier, Pierre Mineau, and János Világosi	292
BOOK REVIEW. Edited by Jeffrey S. Marks.....	294

NUMBER 4

RESPONSES OF NESTING BALD EAGLES TO EXPERIMENTAL PEDESTRIAN ACTIVITY. James W. Watson	295
DISPERSAL AND MORTALITY OF RED-SHOULDERED HAWKS BANDED IN OHIO. Cheryl R. Dykstra, Jeffrey L. Hays, Melinda M. Simon, John B. Holt, Jr., G. Ronald Austing, and F. Bernard Daniel	304
DECREASES IN A POPULATION OF RED-SHOULDERED HAWKS NESTING IN CENTRAL MARYLAND. Elwood M. (Woody) Martin	312
SEASONAL VARIATION IN SEX RATIO OF NESTLING ELEONORA'S FALCONS. Dietrich Ristow and Michael Wink.....	320
TAWNY FISH-OWL PREDATION AT FISH FARMS IN TAIWAN. Yuan-Hsun Sun, Hsin-Ju Wu, and Ying Wang.....	326
GEOGRAPHIC VARIATION IN MORPHOLOGY OF FOUR SPECIES OF MIGRATORY RAPTORS. Elise Vernon Pearlstine and Daniel B. Thompson	334
HOME-RANGE SIZE OF THE JAVAN HAWK-EAGLE (<i>SPIZAETUS BARTELSI</i>) ESTIMATED FROM DIRECT OBSERVATIONS AND RADIOTELEMETRY. Jan Ove Gjershaug, Nils Røv, Torgeir Nygård, Dewi M. Prawiradilaga, M. Yayat Afianto, Hapsoro, and Adam Supriatna	343
POPULATION STATUS AND REPRODUCTIVE PERFORMANCE OF EURASIAN GRIFFONS (<i>GYPES FULVUS</i>) IN EASTERN SPAIN. Pascual López-López, Clara García-Ripollés, and José Verdejo	350
SHORT COMMUNICATIONS	
GENDER DETERMINATION IN THE SWAINSON'S HAWK (<i>BUTEO SWAINSONI</i>) USING MOLECULAR PROCEDURES AND DISCRIMINANT FUNCTION ANALYSIS. José Hernán Sarasola and Juan José Negro	357
PRODUCTIVITY AND FLEDGLING SEX RATIO IN A CINEREOUS VULTURE (<i>AEGYPIUS MONACHUS</i>) POPULATION IN SPAIN. Auxiliadora Villegas, Juan Manuel Sánchez-Guzmán, Emilio Costillo, Casimiro Corbacho, and Ricardo Morán	361
NEST PROVISIONING OF THE ORIENTAL HONEY-BUZZARD (<i>PERNIS PTILORHYNCHUS</i>) IN NORTHERN TAIWAN. Kuang-Ying Huang, Yao-Sung Lin, and Lucia Liu Severinghaus.....	367
WINTER DIET OF THE GREATER SPOTTED EAGLE (<i>AQUILA CLANGA</i>) IN THE AMVRAKIKOS WETLANDS, GREECE. Haralambos Alivizatos, Dimitris Papandropoulos, and Stamatis Zogaris	371
GENDER DETERMINATION OF EURASIAN EAGLE-OWLS (<i>BUBO BUBO</i>) BY MORPHOLOGY. Maria del mar Delgado and Vincenzo Penteriani	375
LETTERS	
A POSSIBLE CASE OF DOUBLE BROODING OF EAGLE-OWLS (<i>BUBO BUBO</i>) IN SPAIN. Joaquín Ortego.....	378
INSECT HAWKING OBSERVED IN THE LONG-EARED OWL (<i>ASIO OTUS</i>). Darren J.H. Sleep and Rowan D.H. Barrett	379
OSPREY SCAVENGES COMMON MURRE CARCASS IN COASTAL WASHINGTON. Joseph B. Buchanan	380
HOW LONG IS TOO LONG? A CASE OF FOSTERING NESTLING BONELLI'S EAGLES (<i>HIERAAETUS FASCIATUS</i>). Satish A. Pande, Amit P. Pawashe, Banda Pednekar, Anil Mahabal, and Reuven Yosef	381
INFORMATION FOR CONTRIBUTORS	383
INDEX TO VOLUME 38.....	387



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RAPTOR RESEARCH FOUNDATION, INC.

Grants and Awards

For details and additional information visit: <http://biology.boisestate.edu/raptor/rrfi.htm>

Awards for Recognition of Significant Contributions.

The **Tom Cade Award** is a non-monetary award that recognizes an individual who has made significant advances in the area of captive propagation and reintroduction of raptors. The **Fran and Frederick Hamerstrom Award** is a non-monetary award that recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Submit nominations for either award to: Dr. Clint Boal, Texas Cooperative Fish and Wildlife Research Unit, BRD/USGS, Texas Tech University, 15th Street & Boston, Ag Science Bldg., Room 218, Lubbock TX 79409-2120 U.S.A.; phone: 806-742-2851; e-mail: cboal@ttu.edu

Awards for Student Recognition and Travel Assistance.

The **James R. Koplín Travel Award** is given to a student who is the senior author and presenter of a paper or poster to be presented at the RRF meeting for which travel funds are requested. Application deadline: due date for meeting abstract. Contact: Dr. Patricia A. Hall, 5937 E. Abbey Rd., Flagstaff, AZ 86004; phone: 520-526-6222 U.S.A.; e-mail: pah@spruce.forest.nau.edu

The **William C. Anderson Memorial Award** is given to both the best student oral and poster presentation at the annual RRF meeting. The paper cannot be part of an organized symposium to be considered. Application deadline: due date for meeting abstract, no special application is needed. Contact: Rick Gerhardt, Sage Science, 319 SE Woodside Ct., Madras, OR 97741 U.S.A; phone: 541-475-4330; email: rgerhardt@madras.net

Grants.

Application deadline for all grants is February 15 of each year; selections will be made by April 15.

The **Dean Amadon Grant** for up to \$1000 is designed to assist persons working in the area of systematics (taxonomy) and distribution of raptors. The **Stephen R. Tully Memorial Grant** for up to \$500 is given to support research and conservation of raptors, especially to students and amateurs with limited access to alternative funding. Agency proposals are not accepted. Contact for both grants: Dr. Carole Griffiths, 251 Martling Ave., Tarrytown, NY 10591 U.S.A.; phone: 914-631-2911; e-mail: cgriff@liu.edu

The **Leslie Brown Memorial Grant** for up to \$1400 is given to support research and/or the dissemination of information on African raptors. Contact: Dr. Jeffrey L. Lincer, 9251 Golondrina Drive, La Mesa, CA 91941, U.S.A.; e-mail: JeffLincer@tns.net